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Volume 168 Number 3

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THE NAPLES ZOOLOGICAL STATION AND THE MARINE BIOLOGICAL LABORATORY: ONE HUNDRED YEARS OF BIOLOGY

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PREFACE

The Stazione Zoologica of Naples was founded in 1872; the Marine Biological Laboratory received its first students and investigators in Woods Hole during the summer of 1888. That each has survived is surprising; that they have survived these tumultuous hundred years of science not merely intact, but with steady growth of influence worldwide, is remarkable. There were close and cooperative relationships among leading scientists of the two laboratories during the decades between 1890 and the outbreak of the first World War. Cooperative relationships have continued, but the years of the last century's turn were momentous ones for what became "modern" biology. What went on at the Stazione and at the MBL is thus of great interest as intellectual history *and* for the lessons to be learned about the role of institutions, as such, in the advance of science.

In October of 1984, a meeting was held at the Stazione's ecology laboratory on the Island of Ischia (which laboratory was once a villa belonging to Anton Dohrn, the Stazione's founder). With timely assistance from the Commonwealth Fund, the Klingenstein Fund, and Italian agencies supporting the Stazione, a group of European and American scholars—historians of science and biologists in about equal numbers—met to review the events, the ideas, and the personalities of a hundred years of biology at the two places. As is generally known, the two ostensibly "marine" laboratories have had impact on far more than marine sciences in that interval.

The participants could barely scratch the surface of an immense subject, many of whose source materials are still unexamined. But there was general agreement on its importance and on the opportunities for new and significant research. Thus the Ischia meeting and its contributions were meant to serve rather more than the normal purposes of a scholarly gathering: they were and are meant to be a goad and catalyst for new historical research, and to act thus upon working biologists with a taste for history as well as upon historians of biology and medicine.

Such efforts are rarely successful: historians and experimental scientists (and administrators of science) often fail to communicate. They have different styles of work and different imperatives. The specialties have diverged greatly during their professionalization of the past twenty-five years. The high standards of one group are not necessarily of interest or importance to the other; and what is inexcusable as form for one can be perfectly acceptable to another scholar.

The Ischia meeting was, nevertheless, a success. It included contributions from both categories of participant that were exciting and novel to the other: the speakers did *not* speak past one another. Catalysis of new projects was in the air. The auguries for new writing in time for the MBL's 1988 Centennial are strong.

This volume contains the written version of papers presented *viva voce* at Ischia. Their publication is essential for the catalytic purposes mentioned. This posed, however, a problem inherent in the different working styles of historians, archivists, experimental scientists, and administrators. We saw the choice, initially, as one of forcing all the papers into one or the other mold: that of an historical journal or that of a biological journal such as THE BIOLOGICAL BULLETIN. In the end we rejected both, for it seemed to us more important to communicate the events and flavor of the Ischia meeting accurately than to dress up the biologists' presentations to fit the style of historical scholarship or the reverse. The chapters of this volume

Ischia participants left to right: J. D. Ebert, J. Maienschein, M. V. Bennett, G. Allen, C. Groeben, P. Gross, N. Reingold, J. Z. Young, E. Florey, Mrs. Florey, W. D. Russell-Hunter, E. Cohen, S. Cohen, A. Monroy, and F. Ghiretti. Not shown: B. Fantini.

are, therefore, *sui generis:* they are what went on at Ischia, with transduction only from the spoken to the written word.

The well-disposed reader will therefore, I hope, tolerate what might drive a proper editor to fury: as many different forms of bibliographic citation, nearly, as there are papers, and some abrupt transitions of purpose and point of view. So be it: we believe that there is to be gained an invaluable sense of the importance of the subject to different biological interests. Much will be found here that is new, and some well-known stories, or stories assumed to be well-known, are re-told with new insights. The price of novelty is a much greater intrusion of the personalities of the writers than is allowed today in most professional journals.

The papers as printed follow fairly closely, but not exactly, the order of presentation at the meeting. The broad design, established initially by S. S. Cohen and A. Monroy, the organizers, was for an opening session on late-nineteenth century science in general, followed by developments in the characteristic disciplines of the two laboratories: zoology, embryology, genetics, biochemistry, neurophysiology, botany, ecology. These sessions were succeeded by discussions of particular institutional policies and problems, *e.g.,* the role of teaching and the funding of research. There were, finally, a number of informal discussions of present-day issues of organization and policy. This sequence is maintained, on the whole, in the volume.

The participants are grateful to the supporting agencies, and to the Naples and Ischia staff members for their cooperation and characteristic warm hospitality. I am personally grateful to my colleagues, Garland Allen and Jane Maienschein, for their

indispensable assistance in the substantive—and hence serious—editorial work. We all hope that publication of these proceedings will attract more of our colleagues to the subject, and to exploring riches in the archives of both laboratories. There are powerful continuities of purpose underlying the key ideas of modern biology, and those emerge strongly from study of the two institutions. Such continuities do not necessarily emerge from preoccupation, however intense and skilled, with the current literature of biology. Yet there is reason to believe that understanding those driving forces (and, yes, intellectual prejudices) can be helpful, perhaps essential, for wise decisions about tomorrow's research directions in the laboratory. If the continuities are communicated even to a few readers of this volume, as they have largely ceased to be communicated in graduate biological education, then the efforts of organizing the meeting and assembling this volume will have been rewarded.

Paul R. Gross
Marine Biological Laboratory
March, 1985

Reference: *Biol. Bull.* **168** (suppl.): 4–25. (June, 1985)

ANTON DOHRN—THE STATESMAN OF DARWINISM

To commemorate the 75th anniversary of the death of Anton Dohrn

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Abstract

Based on personal accounts from the Archives of the Stazione, this paper traces the development of Anton Dohrn's personality. His inner motivations, his personal experiences, and the external factors and traditions that led to the foundation of the Naples Zoological Station are described.

Dohrn strove for a greater degree of organization in science. The paper investigates the factors helping to achieve this goal and outlines the influence that the Naples Station had on the foundation of other institutions.

Discussion

In youth we plume our fancy's wings
To flit from sun to sun;
At length we fold them up, and then
A little work is done.
Compared with our imagined deeds
How small and poor it seems!
But then—one little act outweighs
A thousand glorious dreams.

Charles Grant[1]

Anton Dohrn (1840–1909), founder of the Stazione Zoologica in Naples, once said: "To create, to organize, to develop—this is my need, even passion."[2] It is on these motivations that I shall focus in the following presentation.

The Naples Zoological Station was an offspring of Anton Dohrn's personality. Dohrn has been defined as "an independent pioneer of science politics" (Heuss),[3] "a catalyst in the encouragement and stimulation of creative ideas" (I. Müller, 1975, p. 193), and also as being gifted with "an unusually sure eye for the significance of the different sections of our science, and for the way in which they interrelate and complement each other" (Th. Boveri, 1910, p. 31). Dohrn's personality dominated and catalyzed the activity and the work carried out at the Station, from its founding until long after his death in 1909.

In 1975 O. Skalovà, in her sociological case study of the Naples Zoological Station, contacted 2000 guest scientists who had worked at the Station during the previous 40 years. From the 650 who replied it was clear that one of the most highly rated factors was "the creative atmosphere" prevailing in the laboratory (Skalovà, 1975, pp. 26–28). This atmosphere undoubtedly went a long way to making the Zoological Station a "permanent Congress of Zoologists," as Theodor Boveri called it in his 1910 commemoration of Anton Dohrn (Th. Boveri, 1910, p. 40).

I have long attempted to discover the factors that led to, or that help to maintain, the much-discussed "creative atmosphere" of the Naples Zoological Station. It was

a peculiar condition in which most scientists became engulfed but could not explain. It emanated in the first instance from Anton Dohrn. The intriguing question is how this catalyzing process actually worked, or better, how the personality of Anton Dohrn brought about such a sense of creativity in others. It is also important to analyze the external and internal factors, that contributed to the foundation of a research institute where, in the words in Hans Driesch in 1909, "$^{9}/_{10}$ of all basic work in modern zoology has been done" (Driesch, 1909, p. 514).

Much has been written on the foundation and the history of the Naples Station (Kofoid, 1910; Groeben and Müller, 1975; Müller, 1975, 1976; Partsch, 1980; Müller and Groeben, 1984). In 1940, Theodor Heuss published an exhaustive biography of Anton Dohrn (Heuss, 1962); and the scientist Dohrn and his relation to the zoology of his time has been excellently described by Alfred Kühn (1950). Yet, the question of the influence of Dohrn's personality on the scientific work of the Station remains unexplored.

Anton Dohrn's relationship with his father Carl August Dohrn (1806–1892), a well known amateur entomologist (Heuss, 1962, pp. 23–49; P. Dohrn, 1983, pp. 30–81), played an important role in forming Anton Dohrn's character. His search for acknowledgment among his peers and his essential loneliness as an adult date from his childhood, as do his liberal views, his interest in people, and his wide knowledge of literature, music, and science.

The relationship between Carl August and Anton Dohrn was difficult and tormented, ranging from heated discussions, ruptures, and disinheritance to reconciliation and eventually mutual respect. Dohrn was struck by his father's brilliance and knowledge, and his wide-ranging correspondence with eminent scientists. He longed to live up to his father's expectations, hoping to win his respect and love. In 1897, on the occasion of the 25th anniversary of the Naples Zoological Station, Anton Dohrn acknowledged his debt to his father, his "intellectual protoplasma," but he also noted that in their family circle it was more important to remember quotations from Goethe or to recognize music from Beethoven, than to excel in Greek or mathematics (A. Dohrn, 1897, p. 34).

After having received a humanistic education, Dohrn studied medicine and zoology at Königsberg, Bonn, Jena, and Berlin, obtaining his Ph.D. at Breslau in November 1865. He became *Privatdozent* at Jena in January 1868. To friends he admitted:

> I have no vocation as a Zoologist. You see, to pass my whole day observing through glasses whether this crab has seven or eight segments, whether here lie cells with two or three nuclei, whether this tissue has grown thus or thus—this I can't do.[4]

He was always prone to bigger thoughts, to more grandiose schemes.

Dohrn's attitude suddenly changed, when through the influence of Ernst Haeckel at Jena in 1862, Dohrn became acquainted with Darwin's works. As he exclaimed in the letter of 1866, cited above, "[I felt] a really piercing excitement;" the once dry Zoology was no longer an end in itself, but a new tool to acquire knowledge. The way Dohrn put that new tool to use was through the study of morphology: that branch of zoology in which fields such as comparative anatomy, embryology, and physiology were used as a means of elucidating the phylogenetic history of various groups. Comparative embryology became a cornerstone of morphology, based on Haeckel's recapitulation theory: that the individual in its embryonic development passes through the major stages of its own evolutionary past. Morphology thus became one of the major ways in which zoologists sought to expand and

develop Darwinian theory in the last 30 years of the nineteenth century. As a result of his conversion to evolutionary theory in the early 1860's, Dohrn promised to dedicate his whole life to Darwinism—a promise he indeed kept.

In 1865, Dohrn accompanied Haeckel on his famous expedition to Helgoland where, for the first time Dohrn studied marine organisms (Fig. 1). It seems to have been in Helgoland, while struggling home with buckets full of sea water, that Dohrn and Haeckel talked about a "Zoological Station" (Uschmann, 1959, p. 65). Dohrn's friendship with Haeckel ended a few years later when the younger man, influenced by Kant and F. A. Lange's *Geschichte des Materialismus* (1866), could no longer subscribe to Haeckel's philosophical generalizations. But familiarity with marine organisms as objects for study, and the idea of establishing a marine laboratory remained an important legacy from Haeckel for the rest of Dohrn's life.

In 1867 (July–September) and again in 1868 Dohrn went to Millport, Isle of Cumbrae, Scotland, to continue his studies on Arthropoda. There he lived as a guest of David Robertson (1806–1896), a self-taught Scottish zoologist and later founder of the Millport Biological Station (1885).

It was during this first trip to England that Dohrn, through an introduction by his father to the entomologist Henry Tibbats Stainton (1822–1892), met many English zoologists, most importantly Thomas Henry Huxley (1825–1895), with

FIGURE 1. Excursion to Helgoland, 1865. Standing, left to right: Anton Dohrn, Jena; Richard Greef, Bonn; Ernst Haeckel, Jena. Sitting, left to right: Salverda, Delft; Pietro Marchi, Florence. (Reproduced with permission from: Uschmann, 1959, fig. 23.)

whom a close and warm friendship developed. Huxley even suggested a visit to Charles Darwin (1809–1882), but Dohrn only sent Darwin his publications at that time. This led to an exchange of letters (Dohrn did meet Darwin two years later, in September 1870; see Groeben, 1982). Dohrn also reported on his work at the annual meeting of the British Association, held that year (1868) at Dundee.

Dohrn's close ties with British scientists were to pay off in future years. During the difficult period (1870–1874) when he was trying to build the Zoological Station, Dohrn received the greatest encouragement and help from his British colleagues. Apart from the active support of Darwin and Huxley, Dohrn found a great source of strength and encouragement for his dream of a marine laboratory in the British natural history tradition and the readiness of the British to accept adventurous and even somewhat eccentric plans.

In the period after 1860, stimulated particularly by French and British exploring expeditions, general interest in the sea and its riches and in the potential of marine organisms for systematic and morphological study had increased greatly throughout Europe (Deacon, 1971; Rice and Wilson, 1980). In 1870 at the annual meeting of the British Association in Liverpool, a Committee was formed "for the purpose of promoting the foundation of zoological stations in different parts of the world" (Report, 1871; Dohrn, 1872a; Rice and Wilson, 1980). Indeed, it was this committee, through its many reports as well as notes and articles regularly published in *Nature*, that gave such widespread publicity in the English-speaking world to Dohrn's Stazione Zoological.

In Germany the general concepts of using marine organisms for biological research was first promoted by Johannes Müller (1801–1858). Through his numerous visits to the North Sea (1843, 1848, 1854, and 1855) and especially the Mediterranean (in 1849 at Nice and Villefranche, 1850–52 to Trieste, in 1853 at Messina, 1856 at Cette and Nice), Müller publicized widely the concept of marine biological research as a means of elucidating fundamental biological concepts. Müller was a gifted teacher, with whom most of Germany's principal zoologists and physiologists had studied (Kühn, 1950). Thus, his interest and influence was of considerable importance.

After the British Association meeting in 1868, Dohrn returned to Millport, where, together with David Robertson he constructed a portable aquarium, to take with him to Messina, Sicily, where he planned to spend the winter of 1868–69.

The Straits of Messina were famous at that time for the richness and variety of their marine fauna and flora. In 1788, Spallanzani had studied the pelagic fauna of the area, followed many years later by the German zoologist August D. Krohn (1846). And, Johannes Müller must have conveyed his enthusiasm for seaside studies there to many of his students, since Messina soon became, according to one report, the "Mecca of the German Privat-Dozent."[5] So favorable were collecting conditions at Messina, for example, that in one year (1859–60), Haeckel (also one of Müller's students and inspired by him to do marine investigations), discovered more than 144 new species of *Radiolaria* in the straits.

Messina was thus the obvious choice for Dohrn to conduct marine studies. There Dohrn met up with his friend, the Russian zoologist Nikolai N. Miklouch-Maclay (1848–1888), also a former pupil of Haeckel, and later to become an eminent anthropologist (Müller, 1980). Maclay introduced Dohrn to the Russian-Polish family, de Baranowski, whose eldest daughter Marie (1856–1918) was to become Dohrn's wife in 1874.

Dohrn and Maclay rented two rooms at the Palazzo Vitale, Strada Garibaldi, right on the port, with a breathtaking view of the Straits of Messina and the coast of Calabria. They bought some chairs and had two work-benches made for them. Commenting on their simple life, Dohrn wrote in 1868:

> . . . and so we live, including service and meals, for 5 francs a day, much cheaper and better than at a Hotel, where we would have had to climb 3–4 floors and would also have had difficulties because of our working problems. The fishermen invade our flat and bring us lots of animals.[6]

The portable aquarium Dohrn had built in Scotland proved to be very valuable indeed. For the first time he could observe the breeding of crustacean eggs. However, faced with such difficulties as bad weather, lack of animal supply, and lack of literature, Dohrn realized how useful it would be for scientists to arrive and find the "table laid" for their work (Fig. 2). That is, to find on arrival instruments, rooms, service, chemicals, and books available together with records of where and when certain species could be found and useful information on local conditions, etc. In this spirit he left his equipment and diary at Messina where friends promised to take care of them. In February 1869 Dohrn could thus write to his father: "The Zoological Station of Messina has now been established. I retain it an important progress for our Science should we succeed in getting beyond the embryonic stage."[7] Dohrn and Maclay had optimistically planned to cover the world with a network of Zoological Stations. Although Dohrn thought initially of Venice, Nice, Gibraltar, Portugal, Ceylon, Australia, and the Cape of Good Hope[8], in the end Naples was all he could successfully accomplish.

The potential of marine organisms for morphological and systematic studies had already led several scientists to try to establish study facilities near the sea, *e.g.,* the French stations at Concarneau (1859), Arcachon (1863), and Roscoff (1872). However, these were mostly field stations, connected to a University or Institute, and were not independent facilities to house a host of different sorts of investigations and a wide variety of projects.

Dohrn always acknowledged Vogt (1817–1895) as his forerunner. In 1852, Vogt had tried at Villefranche, and in 1863 at Naples, to found a research and observation station (Vogt, 1871; Dohrn, 1871, pp. 6–8; Oppenheimer, 1980). Neither had materialized, however.

Leaving Messina in April 1869, Dohrn returned to Jena for his summer term lectures and also to collect money for a small building to be constructed at Messina to house the equipment. In so doing Dohrn put to work his "creative imagination"[9], a quality he was aware of possessing to an unusual degree.

Dohrn's enthusiasm for Darwinism did little to remove his dissatisfaction with Zoology—research and teaching—as it stood at that time. He felt that his interests were too wide, or Zoology at the University too narrow—to be able to continue his University career. Science in itself and scientific discoveries just didn't stimulate him, or as Th. Boveri put it (1910, p. 24):

> he lacked the most elementary urge of a scientist, the urge to observe, to discover hitherto unknown facts, even if they are unknown only to the observer himself. Not that he did not acknowledge the value of new discoveries. But it did not matter to him to make them himself.

Dohrn wanted to make a contribution to advancing Darwinism that would exploit his complex personality and gifts. He once put it like this:

> Proper zoological work has elements that do not appeal to me and do not at all take into account an inner need, which is to occupy myself in a practical way, to make an impact in the outside world, to be of service to others.[10]

And again in 1874, during one of his frequent bouts of deep depression—a heritage

FIGURE 2. N. N. Miklouho-Maclay, letter to Anton Dohrn, January 1869, Messina, describing and illustrating the hardships he had to cope with in order to pursue his studies.[35] (ASZN, Dohrn Archives, *Ba 735*)

from his mother's family—he wrote in an unfinished last will: "In the center of my existence lies, I may say, a passion for helping others, direct or indirect."[11]

The growing interest in exploring life at sea, the need for marine organisms for research in morphology and embryology, Dohrn's own marine experiences, his championing of Darwinism, and his need to prove himself—all these currents converged into the creation of the Naples Zoological Station. Dohrn's attention had turned to Naples because he wanted to connect the Station with an aquarium open to the public, the entrance fees thus providing the means to pay a permanent assistant. Dohrn therefore had to choose a large city that attracted many tourists. Naples at that time was still one of the largest and most attractive cities of Europe with more than 500,000 inhabitants and about 30,000 tourists a year (Vogt, 1871).

In 1870 Dohrn went to Naples; with luck he overcame doubts, ignorance, and misunderstandings and persuaded the city authorities to give him, free-of-charge, a plot of land at the sea edge, in the beautiful Royal Park (today, the Villa Comunale). For his part he promised to build a Zoological Station at his own expense. Dohrn himself gives a very colorful description of his experiences with the Neapolitan authorities in his "History of the Naples Zoological Station," which he started to compile in 1895. (The unfinished manuscript is kept in the Dohrn Archives at the Stazione.)

In October, 1871, Dohrn installed himself with all his equipment and books at the Palazzo Torlonia, near the small port of Mergellina in Naples, together with the

biologist E. Ray Lankester (1847–1929). The two friends were thus able to immediately start their scientific research. The foundations of the Zoological Station were laid in March, 1872, while by September, 1873, the whole building was finished (Fig. 3). Two-thirds of the building costs came out of Anton Dohrn's and his father's pockets, the remaining third was provided by loans from friends.

The finished building contained pumps, machines, store rooms, and sea water tanks in the basement; a public aquarium on the ground floor; a large laboratory for about 20 scientists and the frescoe room with the library on the first floor; and 12 smaller labs and living quarters for the custodian and assistants on the second floor. The first scientist to work at the Station, the German anatomist Wilhelm Waldeyer (1846–1921), arrived in late September, 1873.

The first department was that of Morphology, then the dominant branch of biology. In 1876 a botanical department was created. Although there was no room initially in the main building, physiology was added in 1882 by renting a small building near the Station. The space problem was alleviated by adding two new sections to the main station, one in 1885–1888, and another in 1903–1906. A department of bacteriology was added in 1887, while physiology could now expand to include both comparative physiology and physiological chemistry (Figs. 4, 5). In 1906 Dohrn had his son, Reinhardt, build a summer home, the Villa Acquario, on his beloved island of Ischia; today the Villa Acquario houses the Station's Ecology Department.

In order to cover the running expenses of the institute Dohrn devised the so-called "Table-System:" against an annual fee the contract partner (universities, ministries of education, scientific institutions, private individuals) had the right to nominate one scientist to use a table for one year. A "table" included lab space, fresh animal supply, chemicals, and the use of the library and other facilities. All of

FIGURE 3. The Naples Zoological Station in 1873. (Dohrn Archives)

the arrangements, financing, and guidance of day-to-day activities, were supervised by Dohrn himself. To give one example of his successful managerial skill: by 1890, all debt on the original building and the first addition had virtually been paid; the annual balance showed a remarkable profit of 8,000 francs (out of a total of 200,000 francs income); and 36 tables were rented annually by 15 different countries. Dohrn also started a specimen supply program as another source of income. Thanks to the inventiveness and skill of preparator Salvatore Lobianco (1860–1910), who entered the service of the Station at the age of 14, the Zoological Station soon became known for the beauty and perfection of its collections of preserved marine animals. These were sold to museums, institutes, and individuals all over the world, and many samples are still on display in the Station today.

Through lectures, conferences, and written articles Dohrn continuously tried to make the Zoological Station known to a wider public. He always solicited international support as a way of insuring the scientific and political independence of the Station. In Germany Dohrn concentrated on interesting influential politicians, scientists, industrialists, dukes, and kings, always hoping that they would further the interests of the Station. The Naples Station soon became a "must" for every aspiring biologist around the world and for every visitor to Naples. In 1877 the Berlin Academy of Sciences and the Prussian Ministry of Education provided funds for the "Johannes Müller," a 5-ton steam launch which served for both collecting and excursion trips. In fact, important guests to the station were usually taken on an excursion on the "Vaporetto" to one of the many beautiful places in the Gulf of Naples (Fig. 6).

In 1879–80 the Zoological Station started three different publications: the *Mittheilungen aus der Zoologischen Station zu Neapel* (vol. 1, 1879), intended for

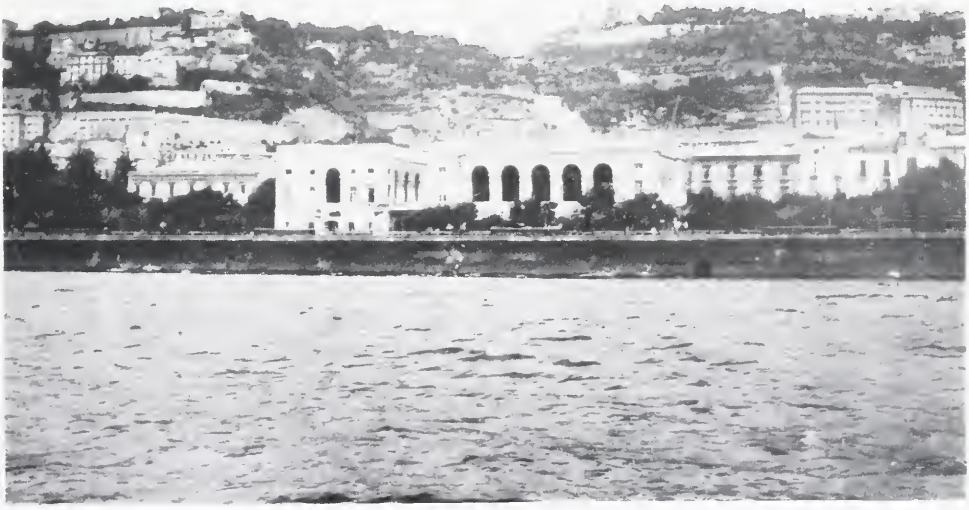


FIGURE 4. The Naples Zoological Station, first and second building. November 1889. (Dohrn Archives)

FIGURE 5. The Naples Zoological Station today. (Photo Lab, Stazione Zoologica)

the research results of staff and guest scientists; the series of monographs *Fauna und Flora des Golfes von Neapel* (vol.1, 1880) as an inventory of the Mediterranean; and finally the *Zoologischer Jahresbericht* (Vol. 1, 1880), a reference journal that soon became famous for its rapid publication and accuracy.

Although Darwin advised Dohrn that establishing a library would be too great an expense and consumption of time (Groeben, 1982, p. 29), Dohrn thought that availability of all the major published sources was a necessity for his research institute. He gave his own large collection to the Station, and got publishers and scientists—among them Darwin—to donate their publications in Zoology and related fields. The Naples Station's biological reference collection is still unrivalled in Europe today (Fig. 7).

Dohrn was also able to obtain some of the latest equipment through donations or at special low prices. For example, Ernst Abbe (1840–1905) of the Zeiss factory, one of Dohrn's few close friends, allowed the Station to purchase sets of Zeiss instruments at a significant discount; in return, workers at the Station suggested ways in which the equipment could be improved, and Zeiss was brought to the attention of the international scientific community (Fig. 8).

Assistants and guests collaborated in improving section-cutting and staining methods, thus maintaining the high level of technical services offered by the Station. As C. O. Whitman (1883) aptly summarized it in his article on "The advantages of study at the Naples Zoological Station," written after he had worked at Naples in 1881–82:

FIGURE 6. "Johannes Müller" (right) and "Frank Balfour" (left), the two steam launches of the Naples Zoological Station, at Mergellina. On the left in the background: the Naples Station. December 1891. (Dohrn Archives)

> [The Station is] a sort of international depot for the reception of discoveries and improvements made elsewhere. The heterogeneous material thus obtained is sifted, systematized, tested, further elaborated and refined and redistributed.

When the 25th anniversary of the foundation of the Zoological Station was celebrated in 1897, nearly 2,000 scientists presented a signed address to Anton Dohrn, saying," . . . that we are incapable of conceiving what the present state of biological science would be without the influence of the Zoological Station" (Dohrn, 1897, p. 13).

In 1872 Dohrn had published the article "Der gegenwärtige Stand der Zoologie und die Gründung zoologischer Stationen" (On the present state of Zoology and the founding of Zoological Stations) (Dohrn, 1872b) in the *Preussische Jahrbücher*, an important cultural journal widely read by the educated public. An Italian translation appeared a few months later in a similar type of journal. This essay is often quoted as one of the classical programmatical writings in zoology, for it lays out clearly and openly the importance of marine stations for the future of biological research—a future that had been seen by Dohrn as early as 1868.

Dohrn explains that since the time of Darwin zoology has entered a new stage, leaving mere systematics behind. Experience had shown, however, that all practical efforts to promote the new direction, especially the study of marine organisms usually ended in a waste of time, money and energy, because, in Dohrn's view [zoology] "lacks organization" (p. 4). He argued that future efforts should concentrate

FIGURE 7. The Naples Zoological Station Library in the frescoe room. The cycle of frescos depicting scenes from Neapolitan life, were created in 1873 by the German painter Hans von Marées and the German sculptor Adolf von Hildebrand. 1895. (Dohrn Archives)

on two topics: the struggle for existence and natural selection; and the recapitulation of phylogeny in the development of the individual (*i.e.*, embryology). The latter was clearly in line with Haeckel's "Biogenetic Law," while the former anticipated the

FIGURE 8. Anton Dohrn in his office at his Zeiss microscope. November 1889. (Dohrn Archives)

study of populations in their environment and animal behavior. In addition, new positions in zoology (comparative anatomy and embryology) were also required to guarantee a new structure, and organization for zoology. Zoological Stations would serve a crucial function as "greenhouses" for young zoologists.

The Zoological Station, by providing such perfect working conditions, fully answered the need for organization that Dohrn saw so lacking in zoology at the time. Good organization contributed to saving money, time, and energy for research. Dohrn wanted to render scientific research possible, but he had no desire to interfere with what was done with the means and tools he put at the disposal of his guests. The creation of such a complex and complicated organism as a research station also answered Dohrn's personal need "to be of service to others." To his satisfaction, he had created something new, and in his own sphere he always felt like a monarch; he compared himself often to Bismarck, whom he greatly admired. Conscious of his achievements, Dohrn liked to call himself "the Statesman of Darwinism."[12]

Dohrn disdained fame and honors, although he wasn't beyond using his own numerous decorations if they could be of use in gaining further support. He hoped, through the small kingdom he had created, to gain power[13] and "to exert a strong influence on the outward conditions of Science."[14] For Dohrn this meant influence on those who made or represented science.

Almost as a *Leitmotiv,* Dohrn in his letters to his wife continuously quotes from the prologue to Goethe's *Faust:* "In the beginning was the deed."[15] While still at Jena he had decided to channel all his efforts into doing, acting, and creating, aware that this meant he would have to forego such other interests as socialism, poetry,

philosophy, and music. Several times Dohrn calls the Station a creation, a work of art, similar to sculptures, poems, or paintings.

At this point we should consider the role of Anton Dohrn's own scientific work and its significance, both for him and for the development of the Station. From 1881 until 1907 he published 25 "Studien zur Urgeschichte des Wirbelthierkörpers," thus following the line of research—phylogenetic studies (*i.e.*, morphology)—for which the Zoological Station had been built. While the Station welcomed new scientific approaches—for example, the *Entwicklungsmechnik*, or "developmental mechanics" of Roux and Driesch—during the nineties, Dohrn remained a morphologist, using the Station's facilities as did any other table-holder. Dohrn's aim was not just to reconstruct the phylogenetic tree of vertebrates; his ultimate motive or "main-spring"[16] was to explain the history of human form, of the physical structure of man. In a letter to E. B. Wilson in 1900, Dohrn well characterizes his scientific approach:

> Phylogeny is a subtle thing, it wants not only the analytical powers of the "Forscher", but also the constructive imagination of the "Künstler",—and both must balance each other, which they rarely do,—otherwise the thing does not succeed.[17]

With Dohrn it was very often imagination that prevailed, which was invaluable when creative talents were called for, but it was ill-fitted for scientific research where conclusions must be drawn from facts, and not facts made to fit into conclusions.

In Dohrn's life, periods of practical activity concerning the Zoological Station were intertwined with periods of intense scientific study. In his scientific work, Dohrn ranged in mood and attitude from vigorous enthusiasm for the broad scope of morphological work (for example, his own particular idea, the Annelid-theory of vertebrate origin), to resigned pessimism during which he limited himself only to establishing facts and details, without hope of ever solving the larger problem of vertebrate origin.

One cannot help feeling that Dohrn's intense activity was psychologically motivated by the desire to prove himself to those who had doubted his ability of ever achieving anything in the way of serious scientific work. Principal among those were his father and his teachers Ernst Haeckel and Carl Gegenbaur (1826–1903), who already at Jena had doubted his qualifications as a scientist, criticizing his superficiality. Dohrn said in 1872:

> I have been ridiculized [sic], laughed at, they have told me that I had no character, that I were [sic] weak,—in short all those amiable flatteries which can bring a man to despair or to fury. Then they doubted my beginnings, called me adventurer and phantast, disbelieved my energy,—now they begin to give me credit, to believe in me, and by and by they will praise me and admire me.[18]

Dohrn was flattered that E. B. Wilson taught his works and theories, especially the *Functionswechsel* (change of function)[19] concept in his student courses at Columbia University. He was especially pleased that while he was at Woods Hole in August of 1897, he was asked to discuss his *Ursprung der Wirbelthiere*.[20] Without wanting to detract from the thoroughness of Dohrn's scientific work, it must be said that research and theorizing was only one part of his life. As he put it in a letter to his wife in 1897:

> I have told you several times that I make a work of art out of life itself . . . I found chaos before me and have created out of that both a practical organism:

> the Station, and a theoretical one, the "Urgeschichte der Wirbelthiere". Each step on the path of these two things I have visioned beforehand, as an artist first sees the complete work of art and then starts to create its parts.[21]

Dohrn's model was Goethe's ideal of harmonic humanity (*harmonische Menschlichkeit*)[22], that is, the unity and harmony between what one *can* do and what one *wants* to do. That Dohrn acquired this balance is shown by the fact that, after having absorbed the directive influences exerted on him during his early years, from about 1870 on, he did not start or maintain any close friendships. By then he relied only on himself. This was true with regard to the Station and also with regard to his family.

Anton and Marie Dohrn had four sons (Boguslav, called Bux, b. 1875; Wolf, b. 1878; Reinhard, b. 1880; Harald, b. 1885) and a daughter who lived only one year (1876–1877) (Fig. 9). Anton Dohrn was a loving and caring father, his letters to his wife are full of plans and projects about how to help their sons' intellectual development; they too were something to be shaped according to his wishes.

Although the administrative and social duties of the Station were a heavy burden for him—and his health suffered in consequence—Anton Dohrn would not share this responsibility. He was convinced that, having to answer only to himself he

FIGURE 9. Anton Dohrn and his family. Standing, left to right: Reinhard (1880–1962), Bux (1875–1960), Wolf (1878–1914), and Harald (1885–1945) Dohrn. Sitting: Marie (1856–1918) and Anton (1840–1909) Dohrn. Naples, *ca.*, 1905. (Dohrn Archives)

could keep the Station free from bureaucracy and could give full range to his "creative imagination."

This also explains why there were no strong or outstanding characters on his staff. Hugo Eisig (1847–1920), Paul Mayer (1848–1923), Wilhelm Giesbrecht (1854–1913), and Salvatore Lobianco were all very efficient in their specific areas and they delivered good research, but they weren't personalities. Strong characters like Nikolaus Kleinenberg (1842–1897) (Müller, 1973), J. J. von Uexküll (1864–1944), or Albrecht Bethe (1872–1954)—to name a few—did not remain long at the Station, possibly because they clashed with the equally strong-willed Dohrn.

Now, how did Anton Dohrn actually formulate, create, and direct his Institute and influence science in general?

First, it should be stressed that Dohrn was a very generous and charming person who was unconcerned by social differences (Fig. 10). He was accepted by everyone: the fishermen at Mergellina and at the Station discussed their problems with him; the German Emperor chatted politics with Dohrn down in the Aquarium; and Carmen Sylva, the Queen of Romania, almost fell in love with him. Dohrn put at ease guests from all nationalities and backgrounds. Hans Driesch reported that Dohrn used to say "Here we are a family" (1909, p. 515); in fact, Driesch, representing a completely new direction of scientific work (experimental embryology), would have had reason enough to feel unwanted, but he did not. Scientific discussion, along with very heated, though enjoyable arguments, were frequent; but they never grew personal.

Dohrn was also good company, taking excursions, enjoying jokes and even childish games. He even installed a billiard-table and bowling-alley at the Station, and also organized concerts and promoted literary discussions at his home. Guests at the "Casa Dohrn" and the Zoological Station thus experienced science and art as the two complementary sides of European culture (Groeben, 1984) (Fig. 11).

Twice Dohrn was offered important chairs in zoology, in 1879 at Naples and four years later at Berlin; both times he refused. He did not like teaching and preferred to exert his personal influence through organizing and administration of science. With regard to the Berlin chair he explained to his father: "Here at the Station I can better influence the development of Zoology, and have in my hands human material that is much riper than students."[23] This wish to mold human material was also reflected in the selection and handling of his staff.

> To get out of people like Eisig, Mayer, Meyer, etc., what is possible, for a great purpose, this is the touchstone of the art of handling people; to find them boring is a very cheap and shortsighted pleasure.[24]

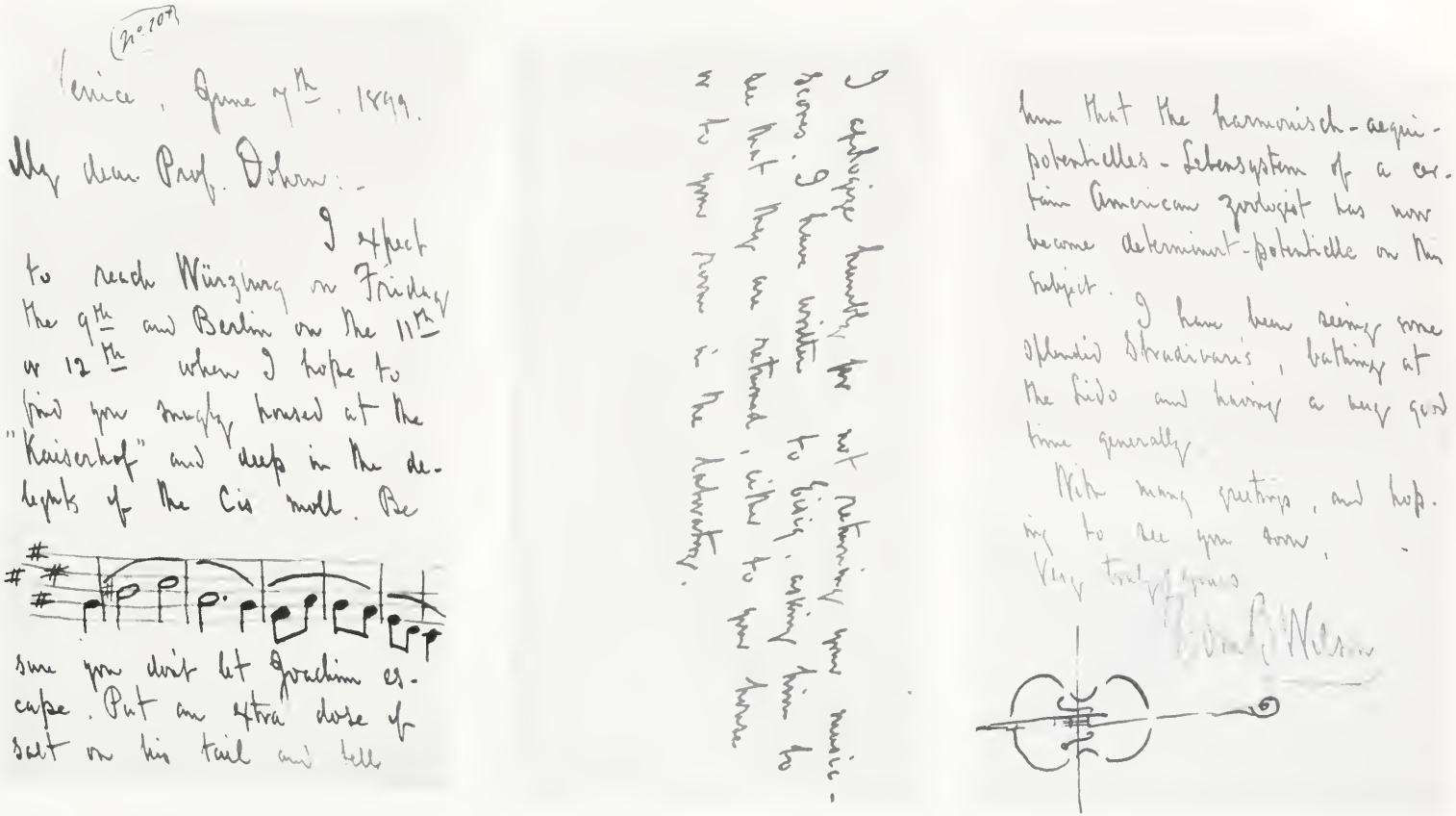
What for many of the guest researchers was a perfect, fruitful, and stimulating stay at Naples, was often directed and organized by Dohrn; one cannot help comparing him to a puppeteer. One example of this is his statement:

> And when I see daily, with how much elan and how much joy all these persons go to work here, who come from outside, and how I succeed through the timely interposition of excursions on the steam-launch to keep up the good humour and high-tensed spirit—then I feel deep joy about the results of hard work and fearful years.[25]

That Anton Dohrn himself was a well-known and respected scientist only contributed to the stimulating atmosphere. From him guests could expect understanding of, though not necessarily agreement with, their work.[26] As a scientist he

FIGURE 10. Anton Dohrn. Sketch by Johannes Martini. *ca.*, 1897. (Dohrn Archives)

behaved as a guest himself, not influencing *what* was done at the Station, only *how* it was done. As an impartial diplomat Dohrn would straighten out technical, scientific, and political wrangles. Unobtrusively, he dedicated more time to professors



Venice, June 7th, 1899.

My dear Prof. Dohrn:-

I expect to reach Würzburg on Friday the 9th and Berlin on the 11th or 12th when I hope to find you snugly housed at the "Kaiserhof" and deep in the depths of the Cis moll. Be sure you don't let Joachim escape. Put an extra dose of salt on his tail and tell him that the harmonisch-aequipotentielles-Lebenssystem of a certain American zoologist has now become determinant-potentielles on the subject. I have been seeing some splendid Stradivaris, bathing at the Lido and having a very good time generally.

With many greetings, and hoping to see you soon,

Very truly yours

Edmund B. Wilson

FIGURE 11. Edmund Beecher Wilson, letter to Anton Dohrn, June 7, 1899, Venice. The friendship between Wilson and Dohrn was based on their love for music. (Dohrn Archives, A, 1899, W.)

than to younger scientists, because he respected their position and personality. He also appreciated their influence in directing their students to Naples, and of course he realized that it was good publicity to attract important figures like August Weismann (who came in 1877, 1882, and 1887), Carl Vogt (who came in 1879 and 1884), and Emil du Bois-Reymond (who came in 1878).

Dohrn was also an excellent public relations man, constantly seeking to extend the name of the Station around the World. For example, he was furious at C. Mereschkowsky, of St. Petersburg, because in several communications of 1882, the latter never once mentioned that his results had been obtained at Naples.[27] Dohrn also tried to promote the name of the Station through solid publications; he did not approve of "preliminary notes" that often led to nothing more, and excluded polemic articles in the *Zoologischer Janesbericht,* making the journal well-respected and a *must* for all libraries and research workers in morphology.

Summarizing, it may be said that as far as the Zoological Station was concerned, the creative atmosphere was something consciously created by Anton Dohrn, who in the process proved himself to be the perfect host or, the perfect statesman of Zoology.

Two main aspects of the Naples Station have inspired the foundation of similar institutes all over the world.

The first "generation" of scientists was mostly impressed by the technical perfection of instruments and service (animal supply, sea water tanks, staining and section-cutting techniques, library) *and* the high standard of research offered at Naples. In the U. S. among the first visitors to the Station were E. B. Wilson, C. O. Whitman, and Emily A. Nunn, all of whom came in 1882–1883, having learned of the wonderful research potentials from European colleagues. Wilson had applied in January, 1883, to visit Naples to work on the development of *Penatulida* "and to learn your beautiful methods of research."[28] After returning to the laboratory of Rudolf Leuckart (1822–1898) in Leipzig, after his stay at Naples, C. O. Whitman had complained, "We have here (at Leipsic) a magnificent building, but nothing to work with. The liberal supply at Naples contrasts strongly with the supply of tables here."[29] And, after returning to the United States, both Whitman and Emily Nunn wrote glowing accounts in *Science* of the Station's opportunities. This did much to spread the reputation of the Station to younger workers in the United States, who subsequently visited Naples in the 1890's and early 1900's (for example, T. H. Morgan, W. M. Wheeler, Nettie M. Stevens, among others).

The idea of a well-equipped marine station for pure research influenced Whitman in his project for a marine station at Woods Hole that concentrated on summer courses. It also guided Kakichi Mitsukuri (1858–1909) in founding the Misaki Marine Laboratory (1887) and E. R. Lankester in building the MBL at Plymouth (1888). And Spencer F. Baird (1823–1887), head of the United States Fish Commission, asked Dohrn for technical information on the installation of the aquarium and the sea water supply in 1875 and 1883, and also for blueprints and advice for the fisheries laboratory he was building at Woods Hole. Anton Dohrn was delighted that Naples had become a standard for others, but he was also anxious to safeguard Naples' position as the "mother-station."

The second feature of the station that so impressed and influenced visitors to the Naples laboratory was its complete freedom of research. This freedom of research, of being host to the international scientific community, is the aspect that has also survived Anton Dohrn's personal imprint. Given his essentially German background and his independent character, the Naples Station could only become a "monarchy," whereas significantly enough C. O. Whitman, from the very

beginning, tried to put the MBL on a democratic basis (Lillie, 1910, p. XXXI). Dohrn's greatness consisted in creating an organism, the potential of which was larger than national, contemporary and socio-political ties.

In 1888 President G. Stanely Hall of Clark University, Worcester, Massachusetts, visited Naples and went to see Anton Dohrn at Berlin. In his first annual report, Hall stressed where Clark University had or had not followed the example of Naples (Clark University, 1891, p. 7; 1893, p. 15).

President D. C. Gilman (1831–1908) of Johns Hopkins University visited the Station in 1890[30] and again in 1902 as President of the Carnegie Institution, which led to the unexpected rent of two "Carnegie-Tables" for American scientists in December 1902.[31]

The Kaiser Wilhelm Institutes (today: Max Planck Institutes) at Berlin were founded as research institutions dedicated to basic science, following the example set by Naples. Through the offices of Julian Huxley (1887–1975) the Naples Station later served as a model for the constitution of UNESCO research programs (Skalovà, 1975, p. 1).

Lastly, one of the most striking examples of the influence that the Naples Station has exerted, concerns the Rockefeller Institute for Medical Research in New York. Simon Flexner (1863–1946), the newly appointed Director of the Institute in 1901, while on a year long recruiting trip through Europe, visited Naples in November 1903 and spent a few days with Anton Dohrn at the Station; here he sought advice, and explained to Dohrn and others about the Institute planned for New York.[32] A few days later Dohrn asked E. B. Wilson in a letter: "A Dr. Flexner was here: he has to do with the Rockefeller Medical Research Institute. What does that mean? Is it a serious and reliable thing?"[33] Flexner on the other hand, in a long letter to Christian Herter (1865–1910), reported on his impressions of Dohrn and the Station. This is one of the rare lively, personal, immediate impressions about Anton Dohrn; therefore, I quote it extensively:

> . . . The most important event of my trip so far has been the meeting of Dr. Dohrn at Naples. Fortunately he was most courteous and permitted me to see a great deal of himself. Besides several meetings in his laboratory where he talked most freely of his plan of organization and its results, he did Helen and me the courtesy to take us for an afternoon's sail on the Bay of Naples in the Station Steamer "Johannes Müller". The afternoon was perfect, the sun shining brightly on a placid sea of the deepest azure blue, and the shores with Vesuvius, Capri and Ischia in the background were of the loveliest tints [?] and form. As some of the Station workers were along I found it easy to pass much of the time speaking with Dr. Dohrn whose large and remarkable experience at Naples supplied an endless fund of entertaining descriptions.
>
> Dohrn is now 63, a large hale man, of large voice and pronounced manners. His love for science is an enthusiasm which is probably greater today than when at 30 he conceived the idea of the Zoological Station—the first station of the kind in the history of the world. He is a great man—of that I have no doubt. I think he impressed me more favorably and strongly than anyone I ever met before. . . .
>
> He advised me to begin in a small way and was delighted with the idea of putting the first force into a small house where the early organization can be completed and from where a move can readily be made into the larger laboratory.
>
> But the advice that he urged most strongly was "freedom". He has never acted as censor to his workers. They come to him, everything is supplied them for their problems, but their results are their own. Any discoveries they make are theirs; and blunders theirs too. "Public opinion, not I, is the censor" was his

repeated statement. "Men work here," he said, "in a dozen different branches of biological science, can I be authority on them all." "No, no, give them perfect freedom; let them search where and how they will; help them in every way that you can, but do not pretend to be master over them." It was a remarkable pronouncement and coming from such an authority and one of the most successful research leaders of the world, worthy of the most thoughtful consideration. And the more I have thought over the subject the more I have come to his point of view. I wonder how it impresses you?

He is putting up now a third building—for Physiology. Of late comparative physiology has grown with such rapidity that a special laboratory is demanded. His enthusiasm in the subject is delightful and he expects important returns from this branch of work. "Dog and Cat physiology" as he called it have about reached their limit of value: what we require is a study of simpler forms for the unravelling of complex phenomena and to render their understanding possible. It was splendid to hear him exclaim over "*Science*" and say again and again in reference to this exertion, or that privation, or a specially striking illustration, "But it is all for Science."[34]

Acknowledgments

I wish to thank Dr. Antonietta Dohrn and Dr. Peter Dohrn, Mr. James Thomas Flexner, and the Rockefeller University Archives for the permission to quote from Anton Dohrn's correspondence, and from Simon Flexner's letters to Christian Herter, respectively.

Notes

[1] Charles Grant (1841–1889), Scottish poet and literary critic and close friend of Anton Dohrn. Dohrn quotes this poem in a letter to his wife as referring to his own life. Anton Dohrn to Marie Dohrn, Aug. 5, 1886, Naples. *Bd 379.* Numbers and letters (*e.g., Bd 379.*) indicate reference numbers of the Archives of the Naples Zoological Station (ASZN). If not mentioned otherwise, quotations are translated from German.

[2] Anton Dohrn to Marie Dohrn, Aug. 1883, Stettin. *Bd 246.*

[3] Th. Heuss, Bemerkungen zu dem Plan einer Anton Dohrn Biographie. 1939. 3 pp., typescript. *Bc. 1939, II.*

[4] Anton Dohrn to Fanny Lewald and Adolf Stahr, April 19, 1866, Jena. *Ba 1178.*

[5] F. de Filippe, quoted by Francesco Todaro in his speech on the occasion of the 25th anniversary of the foundation of the Naples Zoological Station, April 14, 1897. Dohrn, 1897, pp. 5–10: 8.

[6] Anton Dohrn to Fanny Lewald and Adolf Stahr, Oct. 17, 1868, Messina. *Ba 1241.*

[7] Anton Dohrn to Carl August Dohrn, Feb. 15, 1869, Messina. *Bc 16.*

[8] Anton Dohrn to Thomas Henry Huxley, April 24, 1870, Naples, *Ba 473,* and to Fanny Lewald and Adolf Stahr, July 6, 1870, Stettin, *Ba 1278.*

[9] Anton Dohrn to Marie Dohrn, Aug. 1, 1886, Naples. *Bd 372;* and May 15, 1890, Naples. *Bd 681.*

[10] Anton Dohrn to Fanny Lewald and Adolf Stahr, April 15, 1866, Jena. *Ba 1177.*

[11] Anton Dohrn, unfinished manuscript, September 1874, Hoekendorf, *Bd 0173.*

[12] Anton Dohrn to Marie Dohrn, July 1, 1884, Hoekendorf. *Bd 283.*

[13] Anton Dohrn to Marie de Baranowska-Dohrn, Nov. 8, 1873, Naples, *Bd 0114;* Oct. 2, 1881, Berlin. *Bd 207.*

[14] Anton Dohrn to Marie Dohrn, June 6, 1884, Moscow. *Bd 268.*

[15] Anton Dohrn to Marie Dohrn, Aug. 22, 1888, Hoekendorf. *Bd 543.*

[16] Anton Dohrn to Marie Dohrn, Dec. 24, 1889, Naples. *Bd 648.*

[17] Anton Dohrn to E. B. Wilson, Feb. 20, 1900, Naples. *Bd 846* (in English).

[18] Anton Dohrn to Marie de Baranowska, Dec. 31, 1872, Berlin. *Bd 020* (in English).

[19] E. B. Wilson to Anton Dohrn, April 13, 1909, New York. *G.XXXI.46.*

[20] Anton Dohrn to Marie Dohrn, (Aug.) 13, 1897, Detroit. *Bd 1101.*

[21] Anton Dohrn to Marie Dohrn, Aug. 1, 1886, Naples. *Bd 372.*

[22] Anton Dohrn to Marie Dohrn, Dec. 27, 1884, Berlin. *Bd 327/28.*

[23] Anton Dohrn to Carl August Dohrn, May 17, 1883, Naples. *Bc 33.*

[24] Anton Dohrn to Marie Dohrn, July 7, 1885, Naples. *Bd 353.*

[25] Anton Dohrn to Marie Dohrn, April 11, 1890, Naples. *Bd 670.*

[26] Margret Boveri to Theodor Heuss, July 5, 1939, Stockholm, copy for Reinhard Dohrn. *Be,1939,H.*

[27] Anton Dohrn to Marie Dohrn, July 29/30, 1882, Stettin. *Bd 223.*

[28] E. B. Wilson to Anton Dohrn, Jan. 29, 1883, Cambridge. *A,1883,W.*

[29] C. O. Whitman, May 1882. This passage has been copied by Paul Mayer on a letter from J. Barrois (original missing). *A,1882,B.*

[30] D. C. Gilman to Anton Dohrn, Nov. 7, 1894, Baltimore. *A,1894,G.*

[31] From Anton Dohrn's letters and from the Presidential Files of the Carnegie Institution (personal communication, James D. Ebert) it shows that the two "Carnegie-Tables" were rented thanks to the insistence of E. B. Wilson.

[32] Simon Flexner to Anton Dohrn, Nov. 4, 1903, Naples. *A,1903,F.*

[33] Anton Dohrn to E. B. Wilson, Nov. 11, 1903, Naples. *Ba 853.*

[34] Simon Flexner to Christian Herter, Nov. 21, 1903, Perugia. Rockefeller University Archives RG 417 Folder 7a #5. Quoted with permission from the Rockefeller Archives and J. T. Flexner, New York.

[35] Nikolai Nicklolajewitsch Miklоucho-Maclay. Letter to Anton Dohrn, Jan. 1869. Messina *BA 735.* Published in I. Müller, 1980. p. 39.

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AGASSIZ, HYATT, WHITMAN, AND THE BIRTH OF THE MARINE BIOLOGICAL LABORATORY

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Abstract

This paper establishes that the MBL began as a self-consciously American marine laboratory, following the lead of its American predecessors. In particular, Louis Agassiz's School of Natural History at Penikese Island and Alpheus Hyatt's Laboratory for instruction at Annisquam, Massachusetts, directly inspired the MBL. Archival sources reveal the connections and the MBL's goals. Teaching and research were accepted as the dual and compatible goals for the Laboratory, and it was left to the first director, Charles Otis Whitman, to work out how best to combine the two. These emphases and the clientele thus attracted clearly distinguished the MBL from the European laboratories, such as the Naples Zoological Station, which concentrated on independent research. In part the MBL achieved success because both the teaching and research focused on shared basic questions, namely developmental questions posed within a solid morphological tradition. Epigenesis and preformation, the role of cells in development, cell lineage study of early egg organization: such themes ran through most of the work done at the MBL in the first year.

Discussion

Over the years a number of myths have appeared about the early history of the MBL, some better than the truth—as is the way with myths. One such story, reported to the *New York Times*, is representative. There David Starr Jordan, who was then a biologist at Stanford, discussed the founding of the MBL. He reported that "Senator F. Baird, Secretary of the Smithsonian Institution, . . . and his associates met in 1888 and formally organized a corporation, separate from the Bureau of Fisheries, to carry on the work" of marine biology (Jordan, 1926). Fortunately Jordan was a better biologist than he was an historian. Actually Spencer (not Senator) Fullerton Baird had died in 1887 so was unlikely to have done much incorporating in 1888. Other myths include the claim that the MBL was simply a copy of the Naples Zoological Station (Lillie, 1944, pp. 14–15).

I shall examine more closely the foundation of the MBL, and concentrate on two points: (1) The MBL was established as a self-consciously American marine laboratory, even while it reflected influence from Naples, and (2) despite the declared desire to include all of biology, it was the concentration of research and instruction around shared concerns, particularly developmental problems, which brought about the MBL's early—and continuing—success.

Beginning with the first claim, that the MBL began as an American effort, I shall discuss briefly the several cornerstones in the lab's foundations. These include the influence of Louis Agassiz, of Alpheus Hyatt, and especially, of Charles Otis Whitman. Others then constructed a strong edifice on the solid foundation.

Agassiz's summer school at Penikese Island provided the initial vital stimulus. As the MBL's first director Whitman said repeatedly, the MBL was a lineal descendent of its genetic ancestors, Agassiz's Penikese School and Hyatt's Annisquam

laboratory (Whitman, 1883, 1903). For some time, Agassiz had considered the prospect of running a summer school to provide students of natural history with practical experience. In 1873, he finally gained financial backing from a wealthy New Yorker and opened the Anderson School of Natural History on Penikese Island. The clientele was to be school teachers who sought field experience to inform their classroom instruction; thus the lab was oriented toward instruction rather than original research (Agassiz, 1885, chapter 25; Wilder, 1907; Morse, 1923; Conklin, 1927; Wright and Wright, 1950; Dexter, 1974). The school opened in 1873 with about fifty attendees. According to one report the women were very "schoolma'amy" and "the gentlemen are not a whit behind" ("Penikese Island," 1873, p. 378). Yet the group appeared earnest and eager, the same reporter acknowledged, and the group included four individuals of particular importance for the MBL: Alpheus Hyatt, William Keith Brooks, Charles Otis Whitman, and Cornelia Clapp. Hyatt was a lecturer rather than a student, and it was Hyatt who was to become the real father of the MBL (Dexter, 1974, p. 159).

Agassiz was a master of publicity and made the first day a real show—unlike the first day at the MBL. The students and a number of guests met on the dock in New Bedford and went together by steamer to Penikese. There all were treated to a dinner in the newly (and rather hastily) constructed buildings and to an inspiring informal convocation. One student admitted that after the guests had departed and the show was over that the reality of the island proved a bit discouraging. There they were stuck on an island about ⅔ mile long and ⅓ mile wide, which was virtually barren of trees or other accoutrements (Anonymous, 1895, p. 21). The student did not have long to fret, however; work began immediately the next morning and consumed all available time for the duration of the summer—except Sundays when most of the students refused to carry out ungodly biological studies.

Some popular accounts give the impression that the students spent their days wandering idly about the island collecting things without purpose. It is true that the instruction was highly individualized, with each student spending a good part of each day exploring, collecting, observing, recording, and generally studying nature rather than books—as Agassiz instructed. Yet good books, not mere repetitive textbooks, did have their place. So did lectures. Agassiz invited a number of important biologists to lecture to the group on a range of natural history topics (*Popular Science Monthly*, 1874). In fact, each day began with structured lectures, followed by an hour or so of dissection. Afternoons often brought freedom to roam and collect, but students spent most evenings attending lectures, dissecting by candlelight, and writing up their notes from the day's work. Such a system obviously worked best for those students capable of framing their own questions and following through with relevant collecting, but Agassiz and his invited speakers helped articulate appropriate problems as well.

Not everyone approved of Agassiz's school. The highly respected British naturalist E. Ray Lankester admitted that what he called "the spasmodic descent upon the sea-coast" offered a very nice vacation for naturalists who could not otherwise afford such luxuries. Such trips might even result in collection of a few new species, he admitted. But, Lankester insisted, "it is not in this way that the zoology of to-day can be forwarded" (Lankester, 1880, pp. 497–499). A naturalist needs to work at settling "important questions," he believed. Even Whitman recalled that at first he found Agassiz's methods unproductive, but that he soon came to admire them and, indeed, incorporated some into the approach of the MBL (Craig, 1910).

Agassiz's Penikese School continued for a second year, despite Louis's death in 1873 and his son Alexander's illness in the second session of 1874. Then it closed.

Not for lack of funds, as Jordan and others have claimed, but more for lack of anyone's having taken the initiative to keep it going (G. R. Agassiz, 1913, pp. 129, 131).[1]

In 1879 one of the Penikese students, Alpheus Hyatt, began another seaside lab in Annisquam, on Cape Ann in Massachusetts (Dexter, 1952; Boston Society of Natural History; Kohlstedt, 1979). This laboratory had a purpose closely following that of the Penikese School. Intended to provide opportunities for science teachers to observe and study marine animals, the lab was also the inspiration of the Boston Society of Natural History and was supported by the Woman's Education Association of Boston. Hyatt served as director, with the Boston Society Assistant B. H. van Vleck (who had been a student at Penikese) as instructor. After two years in Hyatt's house, the lab moved to a separate location nearby in 1881. Then, with the continuing financial aid of the Woman's Education Association, the Annisquam Laboratory operated as a department of the Society of Natural History. Clearly Hyatt's ideals helped direct the effort, but the specific purpose of providing educational opportunities for instructing science teachers came from the Boston Society, for which Hyatt was the Curator. At times the level of the students' commitment and preparation seemed hopelessly low. As Mrs. Hyatt wrote to Alpheus while he was at sea on an expedition, the group was very uninteresting, even tedious. They were essentially raw recruits, hopelessly elementary students who were beginning to drive van Vleck to despair (Dexter, 1956–1957). But the school did attract a few men such as Thomas Hunt Morgan who certainly became a serious researcher and one of the backbones of the MBL.

In 1887, the Woman's Education Association decided that the project had succeeded and that they would withdraw support since they held the goal of seeding projects until they caught on, then leaving them on their own (Hyatt, 1887). The Annisquam project seemed a success. But Hyatt was rather tired and wished to develop an American marine laboratory on an independent basis: an institution separate from the Society of Natural History and from himself as director. He also felt that a new site would prove preferable to that of Annisquam, which was becoming polluted. Thus came the move to Woods Hole.

Why Woods Hole? The answer lies largely with Spencer Baird. For several years, Baird had wanted his friend Hyatt to move the Annisquam school to Woods Hole, which had purer water, more abundant marine life, a congenial setting and, not coincidentally, was home of the United States Fish Commission which Baird headed (Galtsoff, 1962; Boston Society *Minutes*, 1888, pp. 563–564). Baird wanted to attract researchers and students to form a research community at the Fish Commission. In some details he seems to have been influenced by the research emphasis of the Naples Zoological Station, opened in 1872. At first his efforts seemed to be succeeding (Galtsoff, 1962, p. 29; Whitman, 1883, p. 97; Parker, 1946, p. 136). But the connection of the Fish Commission with the government and its mandate to investigate practical fisheries-related questions made it very difficult for him to develop in the same way as the more independent Naples Lab. Baird did attract cooperation from the Johns Hopkins University, which sent Professor William Keith Brooks and some students to the Fish Commission, and from Princeton and Harvard. Yet Baird failed to gain the necessary financial support to

[1] G. R. Agassiz says that Alexander was always against the Penikese lab and that the financial situation became impossible when Anderson withdrew his support after the second year. Letters from Alexander, May 30 and June 23, 1888, indicate that he probably felt—probably not quite fairly—that he had tried to maintain the Penikese and other marine labs and had received no support from others.

attract other researchers and to establish a permanent research lab in the 1880's in Woods Hole.

In 1887 as Hyatt, the Woman's Education Association, and the Boston Society of Natural History began to consider sites for their laboratory, they did find Woods Hole attractive. Baird had helped the Annisquam school by sending specimens. He had urged a friend to buy land, near the Fish Commission, which was held for the benefit of any educational institution that might build there. He had welcomed Hyatt at Woods Hole. When the MBL was incorporated in 1888 the Trustees chose Woods Hole as their site, and looked to the Fish Commission for further encouragement.

With Hyatt as president, the MBL trustees decided to hire Johns Hopkins Professor of Zoology William Keith Brooks as the first director (MBL *Minutes*, 1888, pp. 11–13). Hyatt knew Brooks, and had recommended him for his job at Hopkins (Gilman Papers). Perhaps Brooks would take the job without pay, Hyatt suggested, and perhaps the Hopkins would lend financial support to the laboratory effort. Now, you know that the first director was actually Charles Otis Whitman. After all, there is no Brooks laboratory building at the MBL these days. Brooks turned down the offer. Why, you may ask? Why would anyone turn down the opportunity to become first director of America's first permanent research laboratory for marine biology? Why would anyone reject the chance to summer in Woods Hole?

The Trustees offered no salary at first, but that alone probably would not have deterred Brooks. Who was this man, then, who rejected his chance to become immortalized at the MBL? Brooks was, quite simply, the zoologist with the best job in America at the time. He was the only professor of morphology at *the* American research university. A student of Agassiz's and participant in the Penikese School, he was teacher of Edmund Beecher Wilson, Thomas Hunt Morgan, Edwin Grant Conklin, Ross Granville Harrison, and others who assumed central importance for MBL history and for the history of biology in general. He was also founder and director of the most significant marine research lab in America to date, the Chesapeake Zoological Laboratory, run by the Johns Hopkins (McCullough, 1969; Benson, 1979, 1985; Gilman Papers). The Chesapeake Laboratory was an informal arrangement each summer where Hopkins graduate students, usually accompanied by Brooks, explored marine life in one or another location, ranging from Beaufort, North Carolina to Jamaica or Bermuda (Chesapeake Zoological Laboratory Reports, Gilman Papers). Brooks's reports to the Hopkins President about these sessions reveal his enthusiasm, but clearly show that his leadership style was best for a very few specially selected men at the Chesapeake Laboratory (and one woman, once—Emily Nunn, later Whitman's wife). Brooks liked the summer research trips, and he liked Woods Hole during his visits at the Fish Commission. But Brooks was one of the most unassuming, retiring, and unlikely-to-be-director sorts of men imaginable. Perhaps he lacked vision. He did *not* believe that Woods Hole could support, or should support, two research labs in marine biology. He chose rather to ally the fate of his Chesapeake Zoological Laboratory with the Fish Commission.

After Baird's death in 1887, the next Fish Commissioner, Colonel McDonald, wished to expand investigation at his lab. He encouraged Brooks to work there as a consultant and researcher and to bring a few of his students as well (Gilman Papers). Brooks was happy with the Fish Commission and was therefore never convinced that the MBL was a good idea. He believed in 1888 that McDonald was making progress in improving the Fish Commission as a research facility. No other

lab was needed, he felt, and especially not in Woods Hole. As he wrote of the MBL idea,

> I said all that I could to convince Sedgwick [one of the MBL Trustees] that the Boston Laboratory would be much more valuable if some other place than Woods Hole were selected, so that naturalists might have the benefit of stations at two points, and if McDonald is able to carry out his plans and to open this laboratory to investigators in future years, I do not believe that the other laboratory can succeed.[2]

As I said, perhaps Brooks lacked vision. Presumably his convictions led him to turn down the directorship of the MBL. Perhaps he was also tired after years of running the Chesapeake summer sessions. Perhaps he did not wish to take on a lab with a very weak financial base and fight the inevitable battles for funding, with no obvious general support. Evidently he felt uneasy about having women in his biology classes and laboratories, and women would be hard to avoid at the MBL because of the laboratory's connection with the Women's Education Association. For various reasons, then, Brooks rejected the MBL offer.

Immediately after receiving Brooks' rejection, the Trustees forwarded an offer to Charles Otis Whitman, then director of the Allis Lake Laboratory in Milwaukee, Wisconsin (MBL *Minutes*, 1888, p. 27). Hyatt probably knew Whitman through Whitman's two summers at Agassiz's Penikese school and also from the years that Whitman spent at the Museum of Comparative Zoology at Harvard. Though certainly not as prestigious as the Johns Hopkins, Whitman headed the other American biological research laboratory at the time. Immediately, Whitman accepted the MBL offer. With only vaguely articulated goals, the Trustees instructed Whitman to begin the lab within a few months: to open in July of 1888. They circulated an announcement to solicit students and support.

The Women's Education Association donated the equipment from Annisquam to the MBL and also helped the MBL Trustees raise money for the new laboratory. Van Vleck served as first instructor, as he had at Annisquam, so the MBL maintained connections with its founders. Yet Hyatt led the Trustees in making it clear that change was also in order, that the lab should offer both instruction and individual investigation, and that as director, Whitman should develop the lab as he saw appropriate. As Frank Lillie later wrote, this decision worked well, for in Whitman "the trustees had found a man not only fitted to carry out their purposes but possessing imagination adequate to transform their shadowy ideas, the zeal and determination required to give them form and substance, and the courage to face whatever difficulties might arise" (Lillie, 1944, p. 36).

The first year began inauspiciously. Cornelia Clapp, who had also attended the Penikese School, arrived on time for the new session and found the carpenters still at work building the lab. Whitman had not yet arrived, reportedly because of family illness. No equipment had arrived; it remained side-tracked somewhere along the way. No one had made arrangements for boarding or lodging. In short, there really was no lab. But Clapp, buoyed by her enthusiasm and by the arrival of the other attendees—about half and half male and female—stayed and waited. Finally, the equipment from Annisquam arrived, Whitman appeared, the one laboratory building was completed, and aside from such troubles as tripping at night over the many boulders in the paths, that first session of the MBL proceeded successfully, if quietly.

[2] Letters, Brooks to Gilman, no date, Gilman Collection, and Brooks to Gilman, December 1980, on the need for a summer lab in the southern United States since he did not regard the MBL as satisfactory. Alexander Agassiz, letter, May 30, 1888, shows his opposition to the new laboratory.

During those first years, the Fish Commission proved very helpful in sharing specimens, providing sea water, a boat, nets, etc. And the Fish Commission men (for unlike the MBL group, they were all men) visited and discussed projects. Clapp recorded that Whitman taught basic techniques and how to observe productively and to get results in morphological research. As she enthused about that first year, the year before the appearance of Wilson, Conklin, or Morgan, "The atmosphere of that laboratory was an inspiration; the days were peaceful and quiet; there were no lectures nor anything else to distract the attention from the work at hand" (Clapp, 1927). That she fell in love with the MBL experience is clear from her life-long active association there. This remarkable woman went on to obtain a second Ph.D. degree with Whitman when he became chairman of the new University of Chicago biology department in 1890 (Rossiter, 1982, pp. 19–21, 86, 88). That the MBL succeeded in attracting such loyal and able supporters undoubtedly contributed to its early success.

The MBL had begun. At the same time that the MBL attracted more researchers and students, the Fish Commission began to have problems with private researchers. In effect, the government bureaucracy wanted the Commission to emphasize fisheries research and did not wish to allow private investigators (Gilman Papers). Brooks' predictions about the redundancy and failure of the MBL soon proved wrong; the MBL soon became the preeminent marine lab in Woods Hole and in the United States. With success, the Trustees and especially Whitman began to have greater aspirations for the lab.

So far, it should be clear, this lab had American roots. It was clearly a biological laboratory for America—the first such permanent facility. The particular mix of instruction and research, with the resulting communication among the students, young faculty, and established researchers, was peculiarly American, possible only in a country which had no established hierarchy in research.[3] The inexperienced learned from direct contact with the more proficient. Thus, those who taught the courses at the MBL could introduce a new generation to the problems and methods they saw as important. Many untrained American scientists received that practical learning with nature which Agassiz had sought—as they could not have at the European stations. The democratic control by a corporation of scientists overseen by interested trustees came only after some reform and struggle in 1897, but the organization was uniquely American and surprisingly successful. The lab had achieved truly national support. The links between that character and that of the Naples Station remain to be examined.

I come now to my second theme: that interest in development (broadly conceived) served as an important unifying focus for the MBL. Despite the expressed goal of including all of biology, the success of the MBL depended on the way the shared problems, namely developmental problems, brought the participants to work together and to communicate in an exciting, productive, and cooperative way.

The fact that developmental questions dominated early work at the MBL and to a lesser extent subsequent work as well is not entirely surprising. Both Whitman and Brooks concentrated on developmental questions, and these two exerted the greatest influence on the young researchers who worked at the MBL in the first decades. More generally, the morphological tradition had come to regard marine invertebrates as particularly useful for revealing homologies as well as evolutionary histories, or phylogenies. By 1890, many MBL researchers had focused on the

[3] W. D. Russell-Hunter has pointed out that the Milport laboratory in Scotland offered an example parallel in some respects; this suggestion calls for further careful study.

question of how the egg becomes fertilized and begins development. Specifically, a number of American researchers began to ask whether development follows a pattern which is predominantly inherited or which is acquired and hence emerges only gradually: that is, whether preformation or epigenesis predominates. In particular, Whitman focused on the question: to what extent does the egg cell already experience organization? (Whitman, 1896; Maienschein, 1985).

It is not easy to answer that question. What sorts of things might even count as evidence that either preformation or epigenesis occurs? What sorts of work should be done to attack the problem—careful descriptive observation of prepared materials or experimental manipulations to acquire new sources of data? Such questions led to intense debates by the 1890's, which I do not have time to discuss here. But the intensity of debate and the concentration of research around exciting problems clearly added to the MBL atmosphere.

Whitman believed that some early organization occurs, that the egg is not simply a "blank slate," but he left open the question of how much such organization occurs and whether cytoplasm or the nucleus is the center of organization. He also suggested how to attack such questions, namely through cell-lineage studies (Whitman, 1878, 1887). Cell-lineage does just what it sounds like—traces the lineages of each cell through every cleavage stage until the investigator gets tired of the tedius effort or until the cells become too difficult to identify further.

In 1890, Edwin Grant Conklin was at the Fish Commission examining early developmental stages. He heard that Edmund Beecher Wilson, at the MBL, was doing something similar. So Conklin walked across the street, talked to Wilson, and both were astonished at how closely their results agreed. As Conklin reported, "Wilson was as excited by those results as I was and he reported this to Whitman. Whitman at once sent for me to come over to see him in the office. . . ." (Conklin, 1968, p. 116). Of course, Conklin rushed right over, and Whitman said he would like to publish Conklin's work in his journal, *The Journal of Morphology*. Others joined in, including Thomas Hunt Morgan and Ross Harrison, though they never actually published their cell lineage work (Costello, 1967). As Whitman's student and second director of the MBL, Lillie, said, when Whitman told him of the people working on cell-lineage and of their findings, "I accepted his advice to take up this subject: and worked on freshwater *Unio*," for which he had to take the train back and forth to a little pond in Falmouth, Massachusetts, carrying his heavy wading boots and a heavy bucket (Lillie, 1926). Cell-lineage work served as a rallying point and attracted researchers to the MBL for a specific purpose (Maienschein, 1978).[4]

By the mid 1890's, cell-lineage work had begun to pale. Several researchers at the MBL turned to other morphological questions and to problems of regeneration, and to physiology and related problems (Werdinger, 1980; Maienschein, 1976; Haraway, unpub.). Also, the experimental work of Jacques Loeb and Charles Manning Child in physiology of development and by the German developmental experimentalists began to attract more attention as a possibly productive method for attacking those same questions about epigenesis and preformation, or whether the egg is organized as a mosaic or develops regulatively. Stimulated by successes from Germany and Naples, biologists became increasingly enthusiastic about the promises of experimental manipulation, which seemed to many to offer quicker and more dramatic results than more traditional methods such as cell-lineage work.

[4] Publications in journals edited by Whitman, *Biological Lectures* and *Journal of Morphology*, report the results of the cell-lineage work.

As Herbert Spencer Jennings later reflected, this led to a mad rush toward experimentation by some. He said of the period:

> . . . their tales disagreed radically. They tried for a long time to convince each other, but failed. And the reason was that there was no way of deciding which, if any, of the tales were correct. But what hath the man of science of all his labor and of the vexation of his heart, if it leads to no general agreement, to nothing that can be demonstrated? And so, the zoologists gave it up; they looked upon the works that their hands had wrought, and behold all was vanity and vexation of spirit. Henceforth, they said, we must so work that our results and conclusions can be tested; can be verified or refuted. We must be able to say: Such and such things happen under such and such conditions, and if you don't believe it you may supply the conditions, you may try it for yourself, and you will find it to be true. But that is precisely experimentation; and so they flocked with enthusiasm to experimentation. (Jennings, 1926, p. 98)

This led to a good deal of argument, with experimental evidence cited as proving one or another point of view. As Jennings later reflected, that period seemed a bit like a comic opera with everyone dancing about singing frenetically "You are right and I am right and he is right and all are right" (Jennings, 1926, p. 99). Not everyone had embraced experimentation, of course. And the turn to experimentation did not, in fact, solve all the problems as some had hoped.

The rush to experimentation settled down, but the concern with shared problems remained into the twentieth century. The cross-fertilization of ideas and exchange of methods really did dominate developmental work at the MBL, as revealed in the *Biological Lectures* published from the Laboratory. By 1910, things had begun to change, as they have continued to do since. Research has steadily diverged in different directions with resulting proliferation of more specialized research projects, courses, and publications—which is another story. The early sense of shared developmental concerns, which provided such a strong foundation for the first permanent American marine laboratory has faded, for better or for worse. As Conklin suggested, such changes in biology have not always advanced biological understanding. Biologists, he said, have become a lot like squid. They have come to progress rapidly backwards while excreting large quantities of ink (Conklin, n.d.). Squid, like ink and progress, have played an important role in the MBL's history.

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THE "NEW" EMBRYOLOGY AT THE ZOOLOGICAL STATION AND AT THE MARINE BIOLOGICAL LABORATORY

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> The time will never come when direct interchange of thought and comparison of methods of research will cease to be of the highest importance to the biologist.
>
> —C. O. Whitman. 1883. The advantages of study at the Naples Zoological Station. *Science* **2**: 93–97

Abstract

The Naples Zoological Station was one of the main centers of the revolt against Haeckelian, phylogenetic embryology. On the other hand, the founder of the Station, Anton Dohrn, while being a distinguished embryologist, was an enthusiastic follower of Haeckel's theories. The question discussed here first is that of the interactions between Dohrn and the followers of the new trend in embryology, the *Entwicklungsmechaniker,* among whom Herbst, Driesch, and Boveri were regular visitors to the Station. While Dohrn fully acknowledged the significance of the discoveries arising from the new experimental approach to embryology, he remained faithful to phylogenetic embryology. Examining the interactions between two American biologists most involved in the foundation of the MBL, namely C. O. Whitman and E. B. Wilson, and the leaders of the "new" embryology, we then discuss the effect of these interactions on the development of embryological research at the MBL. We suggest that the main effect was to promote the new conceptual, and hence methodological, approach to the problems of development. The Naples group saw the egg *as a cell* that could be manipulated in an effort to answer questions concerning cell physiology. In contrast, the Woods Hole group was interested in the egg as the starting point of development. This was reflected also in the choice of the experimental material: the sea urchin egg in the former case and the highly "determined" eggs of mollusks and annelids in the latter.

Discussion

The Naples Zoological Station was one of the strongholds of the revolt against Haeckelian, phylogenetic embryology. In fact, it was in Naples that the advocates of the new experimental approach to the problems of development—*Entwicklungsmechanik* and *Entwicklungsphysiologie*—made some of their most important discoveries, thus starting a new era in the study of development. We wish to discuss here the interactions between the followers of the new approach and the founder of the Zoological Station, Anton Dohrn.

Dohrn was an embryologist who moved in the footsteps of Ernst Haeckel and who had immense admiration of Haeckel's scientific achievements. Dohrn wrote, in 1867, that "In Haeckel's *Gesamte Morphologie der Organismen* lies the foundations of a new science" and, later, that "it is to be considered an established fact that the development of an animal in the egg and in the larval condition is a condensed

and sometimes obscured image of the development of its genealogic tree." One of Dohrn's immediate goals was to analyze in detail one of Haeckel's constructions. "In the same way as linguists reconstruct original languages . . . the zoologist should be able to outline a comprehensive picture of the development of an animal group from a large number of embryological data" and hence "to identify the ancestor of the whole group" (Dohrn, 1872). He thought his "*Funktionswechsel,*" which he considered as probably his most important intellectual achievement, was the key to the changes underlying evolution. The essence of this principle is epitomized in two passages: "The way of life is the agent that keeps the shape of the larva until its development has reached the right size and the tissues from which the insect (Flüge) will arise are already there," and

> The succession of functions which are carried out by the same organ caused the change of the organ. Each function is the resultant of many components, one of which is the main or primary function, while the others are side or secondary functions. The lowering of the primary function and the building up of a secondary function alters the overall function—when the secondary function becomes the primary one, the overall function changes and the result of the whole process is that the organ changes [Dohrn, 1875].

As examples he refers to the anterior limbs of crustaceans turning into chelae, to vertebrate gills turning into mouth apparatus.

Dohrn's theory was the target of a vehement attack by Carl Gegenbaur (1876), who dismissed it, in particular rejecting the speculations about the origin of vertebrates from annelids as "a striking example of unscientific comparative anatomy." Hence, it must have been gratifying for Dohrn to receive a sympathetic letter from Charles Darwin (24 May 1875) in which Darwin cautiously expressed his interest in Dohrn's ideas about the descent of vertebrates. Another letter dated 2 February 1875, comments humorously on the theory of the vertebrate's descent from annelids: "I shall be very sorry to give up the ascidians to whom I feel profound gratitude." Dohrn's "*Funktionswechsel*" principle was also endorsed by August Weismann and Emil du Bois-Raymond.

Thus, for Dohrn as for Haeckel embryology was just a tool, albeit a most powerful one, to construct genealogic trees of the various animal groups and eventually to identify the original form from which all groups branched. The embryo as such was uninteresting. Thus, embryology was reduced to an almost sterile mental exercise. Saying this does not imply that all embryological work carried out under Haeckel's influence was worthless. On the contrary, some important discoveries even paved the way for future work. Yet most observations, no matter how important in their own right, were contorted in order to fit hypothetical and unprovable genealogic trees.

Wilhelm Roux violently opposed this approach. The introduction to the first volume of his *Archiv für Entwicklungsmechanik der Organismen* (1894) may be considered the "manifesto" of the new embryology. His views opposed those of Haeckel's, both theoretically and methodologically, and led to an entirely different approach to the analysis of development. The main claim was that *the study of the embryo was interesting in its own right.* A few excerpts illustrate Roux's point. For example, the program is outlined in the opening sentence:

> Developmental mechanics or causal morphology of organisms . . . is the doctrine of the causes of organic forms, and hence the doctrine of the causes of the origin, maintenance and involution of these forms . . . the general problem of developmental mechanics [is] the ascertainment of the formative forces of energies.

> In so far, however, as forces or energies are only known to us by their effects, i.e., every kind of force by its specific *mode of operating,* the problem may be defined as the *ascertainment of the formative modi operandi.*

From these premises follows the conclusion that "The causal method of investigation . . . is *experiment.* '*Certainty*' in causal deduction *can only come from experiment,* either from '*artificial*' or from '*nature's experiment,* such as *variation, monstrosity,* or other *pathological phenomena,*" and particularly important, "*developmental mechanics must, so far as possible, seek to utilize for its own ends, all the ends and ways of causal investigation of organisms and the results thereby attained,* and not, in foolish conceit, cast aside any biological discipline as being useless." On the other hand, Roux did not disdain phylogenetic studies. Indeed

> . . . in accordance with the double course of development, viz. the *phyletic* and *ontogenetic,* developmental mechanics must look for the causes, or *modi operandi,* of each of these two courses; hence an *ontogenetic* and *phylogenetic developmental mechanics* are to be perfected. But in consequence of the intimate causal connections existing between the two, many of the conclusions drawn from the investigation of ontogeny will also throw light on phylogenetic processes . . .
>
> As long as comparative anatomy attempted to establish only the *main course* of development in the animal kingdom, following in a general way the continuous development of forms only through the *classes* of each type, comparison of different forms showed that essentially and unequivocally the same course of progressive development is followed by nearly all systems of organs. But in further approximation of a higher degree, viz., in tracing that development through the orders, families, genera, and species, even to the individual, so many incongruities in the development of organ systems and organs made their appearance, that comparative anatomy has been compelled to call in the assistance of quite a number of developmental mechanical hypotheses, for the correctness of which only experimental tests can give complete security.

And a few lines later . . . "it would be encouraging if comparative anatomists would themselves resort to experimentation for the purpose of solving . . . the problems in which they are interested" (Roux, 1894). These passages, which are generally overlooked or ignored, show that Roux's position was much more open-minded than that of some of his followers. He seems to have accepted phylogenesis in the realm of *Entwicklungsmechanik;* and in fact the last sentence is a plea for cooperation with the comparative anatomists. As we shall see, quite a different attitude from that of Hans Driesch!

The most strenuous and, indeed, uncompromising and arrogant defender of the new movement was Hans Driesch. It is worth citing some passages from a virulent and somewhat amusing article written by Driesch mostly directed against Hugo Eisig and Edmund Beecher Wilson.

> What do the phylogeneticists want then? They cannot even do consistent biological research! Yes! can they do research at all? . . . and yet [phylogenesis] is there but not as a science as it is not even entitled to this name . . . We know what we can do and what we cannot do for the time being. Our opponents think that *they* know what we don't even want to know. With their comparisons they deal with questions that by their very nature we have not dealt with and which in fact cannot be approached . . . we have started to approach scientifically a very small part of morphological problems, others, such as the very important problem of morphological diversities, not at all. We are well aware of the problem of 'Transformation' but we consider it for the time being an impregnable fortress and we address ourselves to 'Developmental Physiology' as here we see the possibility of obtaining results while our opponents represent us as if we thought that Developmental Physiology were all Morphology [Driesch, 1899].

And in a letter to Eisig (28 August 1898) he wrote as an explanation of his attack, ". . . it is *you* that I have as opponent, and not only you, but also Wilson who with his last publication has become a renegade [referring to the 1898 Wilson paper]. This is why I have to deal in the article with persons whom I know closely and esteem personally and scientifically: this is why I had to write it."

How did Anton Dohrn feel about Driesch and the new direction of embryological research which, ironically, had become so centered at the Zoological Station that the leaders (including such people as Driesch, Herbst, Boveri, Morgan, and Wilson) were known in Europe as "*Neapler Entwicklungsmechaniker*?" There are very few testimonies of Dohrn's opinion of Driesch as a person and as a scientist. In a letter to A. H. Davis (10 July 1903 quoted by Heuss, 1962) he expresses his sympathy and understanding for Driesch: "although I cannot follow the weight of his argument, or his point of view and of his conclusions." And a year later he wrote to Wilson:

> If one day he could be persuaded that he ought not to boast, even in a mild way, of the excellence of his intellectual field but to be courteous and magnanimous with other pursuits, he would grow very much in value. I *hope* he will one day be wise enough to feel that; if not his *Persönlichkeit* will never attain the dimensions of his intellect. I have an intense interest in Driesch, though sometimes I wish him a good licking [27 July 1904, A. Dohrn to E. B. Wilson].

Driesch, on the other hand, greatly admired the contribution to biology of the Zoological Station and hence of Dohrn. Indeed, in his memorial address for Dohrn he wrote that the Zoological Station was "the place where most of the cytology and experimental developmental physiology had originated, however in their own right and not as sciences at the service of the theory of descent, and in fact in open contrast with Phylogenesis" (Driesch, 1909).

Driesch was certainly one of the most interesting and influential personalities at the Naples Station beginning with his first visit in 1891 (Driesch, 1951). For a number of scientists who worked at the Station his influence was a decisive factor in their scientific life. Also, it was largely due to Driesch that researchers recognized the great advantage of the sea urchin egg as an experimental tool. Until recently, in fact, 90% of the work on fertilization and a large percentage of all embryological work rested on experiments on the sea urchin egg. Indeed, it had become a widespread belief that "what is true for the sea urchin must be true for all animals." The discovery of the sea urchin egg as an experimental material can be traced back to the work at Villefranche by the Hertwigs, who followed *in vivo* the details of the formation of the zygote nucleus from the fusion of the male and the female pronuclei (Hertwig, 1876). It was, however, due to Curt Herbst and Driesch that embryologists realized how well the sea urchin egg lent itself to experimental manipulations. One of the earliest, and in fact one of the most important breakthroughs, was Herbst's discovery that blastomeres of the cleaving sea urchin egg would be separated from one another after a brief exposure to calcium-free sea water (Herbst, 1908). These experiments paved the way to one of the most fascinating areas of research in embryology, that of cell interactions. Almost at the same time Driesch succeeded in separating the first two blastomeres and showing that a whole embryo could arise from each one of them. This observation, which at first appeared to contradict Roux's results on the amphibian egg, began the long controversy on the mosaic *versus* regulatory organization of the egg. The aggressive method used by Driesch to separate the blastomeres by violently shaking the egg (the embryologists who used Driesch's method were derisively called "egg-shakers") were later superseded by the highly sophisticated microsurgical technique devised

by Sven Hörstadius in the early thirties (Hörstadius, 1973). To this day Hörstadius's work is one of the points of reference for sea urchin embryology. In Theodor Boveri's hands the sea urchin egg proved also to be an excellent material for the study of the nuclear-cytoplasmic interactions in development through the analysis of the hybrid combinations, a method further developed by his student Fritz Baltzer and still widely used (Baltzer, 1967). (The unfinished manuscript of Boveri's last work on the development of merogonic and partially merogonic sea urchin hybrids is preserved in the MBL Library.) The sea urchin egg was equally important for the study of physiological and biochemical problems, not only those specifically related to development but also those of a more general character. In this context, Otto Warburg's work has a special prominence. His discoveries of the change in the respiration of the sea urchin egg as a result of fertilization started a new field of "chemical embryology," a research line pursued at the Zoological Station primarily by John Runnström and his school (Warburg, 1910). Runnström was indeed a frequent visitor to the Station almost to his death.

In Woods Hole, however, experiments on the sea urchin egg did not start on a large scale until Jaques Loeb's discovery of artificial parthenogenesis (1899), and until Frank Lillie became interested in fertilization early in 1900 [even though Wilson had shown how well-suited the sea urchin egg was for the study of fertilization and cell division (Wilson, 1895)]. This reflects the different kinds of problems which the embryologists in Woods Hole were considering. In Naples, largely under the influence of Driesch and Herbst and later Boveri, interest focused on what Driesch called "developmental physiology," or the study of mechanisms controlling the early stages of development. Woods Hole embryologists, mostly under the influence of Charles Otis Whitman, were interested in the "program of development" and hence primarily in cell lineage. They were interested in the egg and the oocyte as the point of departure for development. The problem of "promorphology," which was completely alien to the Naples group, was central to the Woods Hole embryologists.

The few documents available suggest that Dohrn was aware of the revolution that was taking place in the field of embryology. He recognized the strength of the tide, but still felt lingering fondness for his "fallen idol." He had to "play the host," and as Director of the Station it was his duty to stay *au dehors de la melee;* to take sides might have endangered the position of the Station. In this connection, Dohrn complained of Froriep's use (Froriep, 1902) of meaningless and empty expressions:

> I see in those expressions only empty schemes of the kind that have greatly damaged the already discredited phylogenetic research, and which one should strenuously avoid, if one want to repel within due limits the highbrowed criticism that phylogenesis receives from the completely differently oriented *Entwicklungsmechanik* or *Entwicklungsphysiologie,* and if one want to strengthen its independent and fundamental importance as a historic-biological discipline [Dohrn, 1904].

Thus Boveri may not have been fair when he wrote:

> Not that he did not recognize the value of new discoveries . . . Isn't it surprising that the rich mine that he himself had opened, has had essentially no influence on his own work? The direction of his research was not determined by any kind of external stimuli, but the specific problems that originated in his mind developed into theories that he then tried to verify with facts [Boveri, 1910].

Let us turn to the question of how and to what extent the atmosphere at the Zoological Station and Dohrn's personality influenced visitors. We shall limit our analysis to only two of the first American biologists to work at the Station: Whitman

and Wilson. Given the role played by these two men in establishing the new trend of embryological research in the United States, rather than their own research contributions, we feel that Whitman should be considered the key figure and in fact "the inspirational leader" (Maienschein, 1978). Whitman visited Naples for the first time from November 1881 to May 1882; ten years earlier than Driesch. When he went to Naples he had already had graduate training with Rudolf Leuckart in Leipzig, and hence he had already been exposed not only to the physiological methods but also to the anti-Haeckel wave already in full swing in Germany, whose most prominent figure was Wilhelm His. At that time Whitman had already published his important paper on "The embryology of *Clepsine*" (Whitman, 1878, 1888).

These dates are important as they show that when Whitman went to Germany he already had certain well-defined ideas and, more importantly, he had already developed working hypotheses as to the problems of development and the methodological approach to them. Whitman rejected the idea that gastrulation was the first important event of the development—an idea that carried much weight in phylogenetic embryology and that had been the cornerstone of the "Gastrea" theory. Whitman was among the first to herald the idea that the study of development had to start from the divided egg. In particular, he maintained that the origin of the germ layers (a topic of fundamental importance to the Haeckelians) could not be properly understood without knowledge of the principal events of cleavage, in particular of the eventual significance of the various blastomeres. This means that the main object of embryology was the study of the history of the embryo, from the egg to the adult, rather than from the embryo to the ancestors (Whitman 1894b, 1895). This was well in line with the approach acclaimed by the new German embryological school. What seems new is that Whitman stressed the importance of the organization of the egg—the promorphology—as the basis to understanding development.

Whitman's views on promorphology, organization and epigenesis are best explained in his lecture "Evolution and epigenesis" (1894a) where he wrote:

> It has become perfectly clear . . . that epigenesis, as now understood, does not cover the whole field. Only the old epigenesis . . . ever pretended to start the development of organisms from the level of inorganic matter. . . .
>
> The indubitable fact on which we now build is not bit of inorganic homogeneity, into which organization is to be sprung by a coagulating principle, or cooked in by a *calidum innatum*, or wrought out by a spinning archaeus, but the *ready-formed, living germ, with an organization cut directly from a preexisting, parental organization of the same kind*. . . .
>
> The essential thing here is, not simply continuity of germ substance of the same chemico-physical constitution, but *actual identity of germ organization with stirp-organization* . . .
>
> Let this 'organization' stand for no more than our neoepigeneticists freely concede, namely, that *original constitution of the germ, which predetermines its type of development and the form which ultimately distinguishes it from other species developing under like external conditions.*

and

> The question does not now turn on either of the old hinges, but on what factors determine the type of development. Instead of asking, are all the parts predelineated? we ask, how are they delineated? Instead of referring development to a *deus ex machinâ*, or accident, we ask, what is the mechanism of the germ which enables it under suitable conditions to grow, divide, differentiate, and reproduce all the complicated details of its own species? We see that every form

> presented in development issues as the *product* of what has gone before and as the *foundation* of what is yet to come. Retrospectively, it is a 'determinate,' prospectively, it is a 'determinant.'

Indeed, Whitman challenged the anti-historical approach of the *Entwicklungsmachaniker,* though not that of Roux. Organisms are the product of a long evolution and hence they cannot be properly analysed, let alone understood, without keeping this fact well in mind. Whitman consequently rejected the view of embryology as only "physiology of development" which was based on the assumption that evolutionary history does not play any part in the explanation of ontogeny. Hence, he made a plea for cooperation between morphology and physiology.

Without any direct sources of information it is impossible to say whether Dohrn and Whitman exerted any scientific influence on one another. Certainly Whitman's 1883 article on the Zoological Station shows that he was strongly impressed by its organization and by the atmosphere that Dohrn had managed to create there yet, as we shall see shortly, he did not share some of Dohrn's principles. Nor is it possible to make any meaningful inferences from Whitman's papers after his stay in Naples. It does seem unlikely that the topic of evolution was never mentioned during their conversations. The most that can be said is that daily contact with Anton Dohrn may have been influential in mitigating the later anti-phylogenetic attitude of the most fervent German *Entwicklungsmechanikers.* This is why it is important that Whitman was in Naples before the Driesch era since he developed his own views without being influenced by Driesch's overwhelming personality.

This experience at Naples was of great importance when Whitman began the Marine Biological Laboratory. Indeed, he brought not only the spirit of freedom he had experienced at the Zoological Station, but also an open-minded attitude to approaches to the problems of development. Nothing gives better evidence of the atmosphere that has prevailed at the Marine Biological Laboratory since its foundation than the *Biological Lectures.* Contrary to Anton Dohrn who, under the banner of freedom, banned teaching, lectures, and debates from the Station, Whitman stressed these aspects. And this is why now, nearly a century later, we have an invaluable testimony of not only how biological research *and thinking* evolved, but of the disagreements and personality clashes that occurred along the way. For this reason developmental biologists owe Whitman a debt equal to that which is owed Anton Dohrn.

Wilson's story is quite different. A student of William Keith Brooks, one of the staunchest Haeckelians, Wilson soon became dissatisfied with the phylogenetic approach to embryology. It is significant that his work ripened during his first stay in Woods Hole. There he met Whitman who took great interest in this research on the development of *Nereis.* It is, however, certain that Theodor Boveri exerted the greatest influence on Wilson, followed by Hans Driesch whom he met in Naples in 1892. It was Boveri who remained his point of reference throughout his life, and it is significant that Wilson's celebrated and classic book *The Cell in Development and Inheritance* (1896) is dedicated "To my friend Theodor Boveri." It is no wonder, then, that very early in his scientific career Wilson was decidedly oriented toward the cellular approach to the study of development, with major emphasis on the nucleus. In *The Cell* he writes:

> The primary determining cause of development is the nucleus, which operates by setting up a continuous series of specific metabolic changes in the cytoplasm. This process begins during ovarian growth, establishing the external form of the egg, its primary polarity, and the distribution of substances within it. The cytoplasmic differentiations thus set up form, as it were, a framework within

> which the subsequent operations take place in a course which is more or less firmly fixed in different cases.

Thus Wilson, as did Whitman, looked at the events of oogenesis as the most important events for the subsequent development of the embryo. This does not, however, make him a "preformationist" in the usual meaning of the word.

A detailed account and discussion of Wilson's embryological work, especially with respect to the problem of cell lineage, is provided by Maienschein (1978). Whitman's influence is felt in Wilson's position toward the evolutionary interpretation of development. Wilson's views are best expressed in the two lectures on the "Embryological criterion of homology" (1894) and "Cell lineage and ancestral reminiscence" (1898a, b). Concerning homology, which was another cornerstone of phylogenetic embryology, his position was indeed similar to Whitman's: . . . "*it is the prospective and not the retrospective aspect of development that is decisive . . .*" This is shown most clearly in the case of the germ layers and the cleavage stages. In the latter case embryonic origin and position are utterly worthless apart from developmental destiny. In all these cases homology is determined "*not by origin but by fate.*" A few pages later, ". . . the events of ontogeny are essentially adaptive, and . . . *the persistence of ancestral reminiscences in development or of similarities in the development of homologous parts is in some way connected with the persistence of ancestral conditions of development*" (Wilson, 1894).

Wilson was also a close friend of Anton Dohrn, but again their correspondence reveals only their respect for each other's point of view and remarks concerning common extrascientific interests. Although our inquiry has not established whether and to what extent Dohrn may have influenced scientists working at the Station, or their influence on him, it does lead to some indications as to why the Naples Station and the MBL developed in different directions. This divergent growth can be traced to the different roles their founders conceived for them. When Anton Dohrn founded the Zoological Station, science in Europe and particularly in Germany, was flourishing as never before and it enjoyed great esteem in social and political circles. The university offered excellent teaching facilities, but here were two things a university could not provide. One was a place where people could work under conditions of complete freedom, meaning that no demands should be made on them. The second was the marine material which was proving increasingly to offer unique experimental opportunities. In the U. S., on the other hand, biology was in a backwater compared to Europe, the cultural center of the world. The Americans felt isolated. This is indeed the *leitmotiv* of the articles that Whitman (1883) and Morgan (1896) wrote on the Zoological Station. Their most urgent need was to educate a class of high caliber scientists who could compete with the Europeans. And, as said before, one of Whitman's greatest achievements was to create the Marine Biological Laboratory primarily as an educational center. Educational meaning, in the broadest sense, a place where the exchange of ideas and collaborations were almost forced upon the investigators through series of lectures and, above all, as a result of their participation in various courses. The Embryology course was one of the earliest and most successful courses, judging from the number of eminent biologists who had their starts there. What was the take-home lesson for the American embryologists who worked in Naples? It seems to be two-fold. First, it was the idea of having a laboratory devoted to research where people had the opportunity to meet and exchange their ideas, a kind of "permanent congress," in an atmosphere of complete freedom. Second, contact with the leaders of the new intellectual and methodological approach to the problems of development gave the Americans new impetus for a fresh approach to *their own* problems.

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THE SCIENCES, 1850–1900, A NORTH ATLANTIC PERSPECTIVE

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Abstract

For an overview of the sciences in the last half of the nineteenth century, a series of tables are presented on the official support of the sciences for Germany, the United Kingdom, and the United States at ten-year intervals plus a set of tables with a similar but more detailed breakdown for the United States. The limitations of the data are discussed and certain subdivisions of the tables are analyzed in terms of both national characteristics and indications of later trends. A review of the United States situation at the turn of the century follows, particularly stressing a few relative differences from the other two nations. The paper concludes with a brief consideration of similarities disclosed by the data.

Discussion

To give an overview of what was happening in the sciences, 1850–1900, this paper will present a series of quantitative data of carefully limited scope. Much of what follows will consist of a discussion of the characteristics of the data, of what the data apparently indicates, and of some general questions arising from these findings. Quantification is not viewed by the authors as necessarily *the* road to historical understanding, let alone as encompassing all significant aspects of the past. Conceptual, institutional, and ideological (in a non-Marxist sense) factors often elude quantitative history. Nevertheless, our data represents another way of slicing the historical pie, and one producing results of reasonable validity and even some heuristic values.

The original computations resulted from the desire of the senior author to extend backward in time the kind of information for the United States given by the National Science Foundation's well known series *Federal Funds for Science* in order to test the veracity of contemporary and retrospective statements about the history of science in the United States and to compare the situations in the North American republic with analogous developments in Europe. Known, existing published American sources only permit a limited extrapolation back to the late 1930's; all known earlier data for this century are patchy and flawed to a point of near uselessness. For the last century, an attempt was made to gauge the development of a professional scientific community using numbers derived from studies of the historical bibliography of the sciences and from the occupational data given by the decennial U. S. Census. Although lacking a high degree of precision, the findings provided useful orders of magnitude illuminating questions for further research.[1]

The present paper is an extension of the prior effort to the estimation of the official support of the sciences, 1850–1900, stimulated by the existence of two similar attempts for the United Kingdom and Germany: R. M. MacLeod and E. K. Andrews' unpublished compilation for the U. K., "Selected Science Statistics Relating to Research Endowment and Higher Education: 1850–1914," 1976; and F. R. Pfetsch's *Zur Entwicklung der Wissenschaftspolitik in Deutschland, 1750–1914*, (Berlin, 1974). The date span of the paper derives from the U. K. study's

earliest data and the fact that private sector funding became much more consequential in the United States after 1900, making the federal funds a significantly lesser aspect of the whole than for the preceding decades, a situation persisting until the scientific mobilization of World War II. The figures for the United States are taken from published reports of receipts and expenditures of the Department of the Treasury supplemented as necessary by recourse to the published annual reports of the administrative entities. All the data of the three nations are formally comparable as to origins, a fact that proves both a virtue and a hazard to the historian.

The tables are in two sets, one being the comparative accounts, the second consisting of a more detailed breakdown for the United States; in both sets results are given at ten year intervals (1850, 1860, 1870, 1880, 1890, 1900). Presumably, similar detailed breakdowns are possible for Great Britain and Germany. The three-country limitation is regrettable but not fatal, arising from the lack, to our knowledge, of works comparable to Pfetsch and to MacLeod and Andrews. No doubt similar data exists in the official statistics of many nations, if not in unpublished archival sources. The three countries are an interesting sample, consisting of the two leading national scientific communites at the turn of the century plus a significantly rising presence in the world's scientific economy. From other evidence for specific disciplines, notably physics, and for other countries, particularly France, we believe that little, if any, of the general pattern disclosed will require major amendment. Nevertheless, we hope others compile equivalent data for countries like France, Italy, Russia, Japan, Austro-Hungary, Sweden, the Netherlands, and Switzerland.

To maximize comparability, the U. S. data is given by the categories and standards of the United Kingdom and German sources even though this has seriously complicated our labors at a number of points. Pfetsch is far less explicit in explaining his data than MacLeod and Andrews, but we believe this has not vitiated our basic premises. National differences, whether of current compilers or of the historic data, produce interesting problems not always amenable to easy solution. Both the German and British compilations, for example, include their respective patent offices as a "scientific" activity, something we would have excluded and suspect would not have figured in any U. S. computation of the late nineteenth century. We regard the Patent Office as a property-granting entity, not one engaged in research or in the administration of a development program. The resulting swelling of the U. S. figures obscures the entire question of the theory/applications relationship.

Concentrating on official support obviously evades the entire question of the private sector's role in the support of science, clearly an important matter in the United States and in Great Britain (to a lesser extent) in our period and at other times, but of still lesser importance in Germany. Non-official support will be discussed in a few contexts.

Concentrating on governmental support produces two important consequences for the data presented in these tables. The first is that Pfetsch can and must give considerable information on the German states both before and after the founding of the Bismarckian empire. Not only are published sources readily available, but the former states, like today's Länder, play an important role in the political economy of German science. In contrast, for the United States, doing all of the states in existence 1850–1900 is a formidable research task and one of doubtful desirability given the ample indications of the modesty of state and local support relative to federal patronage. Nevertheless, some such support will be appropriately noted in the discussion, and readers should assume that the U. S. figures are understated to a slight but not yet determined degree.

Relying on official sources means using line items as given in each nation's respective national accounts. These do not exactly match. Further, we have encountered many instances where research funding is not differentiated from general allocations. In the U. S. case a number of instances have yielded, after further research, to more precise breakdowns. In general, all three national sets of data are derived from attempts to concentrate on organizations with primary or clear R & D missions or with an R & D support role. In the U. S. case we have excluded instances of routine, non-R & D uses of scientific and technical personnel and made judgments of inclusion based on evidences of scientific sophistication. For clarity and comparability, data are reported by administrative units even though many units will engage in diverse work in terms of subject matter. Since further subdivision is often not possible even with arduous and perhaps dubious estimating procedures, the present array is a useful first approximation with the virtue of informing us of what the past was like in its own terms without a spurious precision deployed anachronistically in the service of today's concepts.

Because of the existence of an extraordinary statistical compilation for the discipline of physics around 1900,[2] for comparability we will similarly report all expenditures in German marks. Throughout this period there was a great stability of exchange rates: 4.2M/$1 and 20.6M/£. All values are current without standardization for inflation/deflation nor have we attempted to normalize for comparative costs of living. For example, the physics data indicates that U. S. figures are overstated in comparison to Western Europe because of higher costs for salaries, supplies, and equipment.

Let us consider specific categories in the comparative national accounts. Fully in keeping with the pride of place accorded in the German rhetoric of the past and in contemporary historic accounts are the large sums reported for the support of higher education by the German states. Yet these impressive sums are far from unequivocal in their meaning. First, the numbers are not limited to research expenditures and include work in humanistic and social science fields, not only the physical and biological sciences. They represent essentially the cost for the maintenance of a system of higher education. In contrast, the "Anglo-Saxons" largely attempt to restrict the sums to scientific and technical education. It is not simply the distinction between German "Wissenschaft" and English "science" but differing perceptions of the relationship of peaks of achievement to the broader cultural infrastructure. We suspect that the sciences were subsumed under a broader rubric like "Kultur" with research and education in "Kultur" being seen as co-extensive. That conjecture is reinforced by a second, related characteristic of the data. Pfetsch asserts that the Imperial government did not generally support "zweckfrei" research. In his analysis what we would designate as pure research is located in this educational sector; in fact all of those funds are designated "zweckfrei." As we cannot conceive of that categorization, there is obviously a differing concept here of the relationship of pure research to application. The two issues raised in connection with higher education crop up elsewhere in the tables; the British occupy a middle position, perhaps somewhat closer to the Germans than to their American cousins. Pfetsch and other Germans of the past do not consider the training of individuals for the professions as a mission and tend to restrict "zweck" largely to whatever effects "wirtschaftswachstum."[3]

Also predictable are the large U. S. investments in knowledge and use of natural resources (lands, forests, agriculture, fisheries), given the obvious drive to settle and to exploit a large continental mass. Two qualifications are pertinent. Given the comparative areas, the German and British sums are hardly disproportionately

small, especially if we remember that the analagous costs for the imperial possessions of Britain are not in these tables but in the separate governmental accounts of India, Canada, Australia, Egypt, etc. Given what is known of similar French and Russian activities, everybody was doing it, not simply the expanding U. S. republic. If there is a crucial difference, it is qualitative. The Americans were particularly adroit here in linking scientific research with efficient technological exploitation. To be more exact, a vast research enterprise arose with a basic research component supported for its own sake and for a belief in its ultimate utility. The Fish Commission, associated with the history of MBL, is a modest example.

Notably absent from the U. S. federal figures are sums for academies and societies. While some state funds went to these bodies, those organizations are overwhelmingly part of the private sector to this day. European observers and some American scientists used to regard this as a serious blemish, disregarding that learned and professional societies were proliferating in the country from 1850 even to this day. Disregarded also is the obvious point that in most western countries in the same period the support and conduct of research have increasingly come in the hands of other kinds of organizations (government bureaus, universities, research laboratories, industrial concerns, etc.). The particular arrangement in the United States has had no obvious deleterious effect on the growth of the sciences. What vexed U. S. scientists from time to time was the sense of a lack of an assured high status in a national hierarchy.

Both III, Medicine and Health, and VIII, Military, have interesting limitations to their data and at the same time are unexpectedly informative. For all three countries, attempts were made to separate out routine hospital and clinical care in favor of medical research and public health administration. Roughly, a distinction was made between prevention and treatment. As far as the sources permit, our data estimates the former. Completely omitted for the U. S., for example, is the hospital system of the Marine Hospital Service (the forerunner of the U. S. Public Health Service) and the medical departments of the Army and Navy. By analogy with the British Local Government Health Board and similar German bodies, we have included the federally funded District of Columbia Health Department. As no American state and local entities are reported, U. S. figures understate the support for this activity. The 1890 and 1900 numbers include a small sum for the Marine Hospital Services' Hygienic Laboratory, the forerunner of the National Institutes of Health. We should note here that Pfetsch, like other Germans, classifies medicine as "zweckfrei," again a categorization we cannot accept.

The military figures probably understate slightly the amount of investment in weaponry. Only rarely are such sums given separately. We assume that R & D for warfare, to the extent actually performed in that era, is largely subsumed under the heading of procurement costs and the like. Much of the U. S. expenditures are for peaceful (or at least, semi-warlike) purposes. Although similar uses were made of the military in other countries, the lack of a serious military threat in the last century coupled with the general sense in the last century of a lack of alternate institutions and a shortage of skilled personnel resulted in the pattern disclosed here. When the security environment changed markedly during and after World War II, it was relatively easy for the defense establishment to assume, openly and otherwise, a substantial role in the support of the sciences.

Finally, the U. K. support of museums is eye-catching. Even making allowances for private sector support in the United States, the sums expended are quite high, quite disproportionate to our subjective sense of the relative merits of contributions from the three nations. We suspect that the U. K. figures represent, in part, the

enduring strength of a wide public interest and participation in natural history in that country. We hesitate to speculate on how this passion for museums aided or hindered the growth of support for experimental and quantitative branches of biology, not to mention geophysics with its quite different approach to the history of the Earth.

To conclude, we will first look at the United States around the turn of the century and then offer observations on a number of characteristics common to the three nations. From Forman, Heilbron, and Weart, we know that in 1900 physics in the United States received 2,990,000 M, partly from state governments but mostly from the private sector. To date, we have not succeeded in obtaining any reliable estimate for research support in general in 1900. Shortly after the turn of the century, the newly established Carnegie Institution of Washington reported that the funds specifically earmarked for the support of research totaled $2,952,642, yielding an annual income of $199,625.[4] But that figure is clearly grossly on the low side, given both the federal numbers and the data for physics. What CIW reported were the relatively few endowments solely designated for research or nearly so, omitting support coming from other, more general bodies of funds. In doing that, the Carnegie Trustees not only exhibited a desire to increase funding ticketed exclusively for research but, as we shall shortly note, acted in accordance with a still persisting national characteristic. Since we know that higher education then and now loomed large in U. S. science, let us consider that class of institutions. In 1900 more than 4% of the 18–21 age group were enrolled in American colleges and universities, a high percentage in terms of European norms of that date. The endowments of these institutions (overwhelmingly private) totaled $166,193,529, yielding an annual income of $11,995,463. To this must be added the considerable sums received for tuition. Although overwhelmingly devoted to instruction, clearly some fraction of higher education's resources went into research.[5]

Obviously, by 1900 the United States of America was engaged in an extensive, if uneven, effort to expand research and development. Certain peculiarities are worth noting with the proviso that they are relative, not absolute, differences. First, the private sector plays a greater role in the U. S., then and now. Second, we infer from our data and later evidence a persisting desire to give priority to erecting a supporting infrastructure, rather than simply to target great men, great ideas, intellectual breakthroughs, or the like. Even so-called "wars" (on cancer) or mobilizations (for defense or space) were accompanied by a concern for expanding facilities and the supply of specialized personnel. We conjecture this arose initially from a sense of deficiency in the national scheme of things and suspect that in Europe a contrary view prevailed at many points in time based on a degree of complacency buttressed by an unspoken motive to perpetuate a desired hierarchical social order.

Third, we are impressed by the relative willingness of the U. S. organizations and institutions to split out research and other activities from otherwise undifferentiated wholes; witness the contrasting treatment of the German university and the Carnegie Institution's narrow focus on research endowments. Partly this arises because Europeans tend to see all these activities as part of a cultural whole, in turn part of a specific stratified social order. The U. S. tendency, (manifested in such seemingly narrow technicalities as the wording of Circular A-21 on research costs), represents a traditional view of a limited role for government requiring, therefore, a careful, often nit-picking analytic differentiation by function, process, intent, origin, even ultimate result. This tendency encourages attempts at precise differentiations of "pure," "applied," "development," and other categories. That such

analyses hardly represent the real world of research and development is quite apparent from the disputes in the United States since World War II over support of university science, the role of health research, and the nature of research and development under the auspices of the armed services. It is not accidental that this is the case; all three—the university, the health sector, and the defense establishment—are multi-purpose continuums whose individual parts make only partial sense isolated from the whole.

All three nations display great overall similarity in their patterns of funding, 1850–1900. Even a difference like the absence of U. S. support for academies and societies is an artifact of data limited to the federal sector. Nor is that surprising as all three are part of a larger entity—Western Civilization—and one can assume an overall tendency to emulate, if not to compete with, successful innovations anywhere, both intellectual and administrative. We are postulating a kind of steady state, a situation now spread to large portions of the globe. Each major scientific country and many lesser scientific nations observe changes in other national communities and very often adjust their national accounts accordingly.

Despite the understandable emphasis in the literature on novelties—conceptual, factual, and applied—what the data shows in this period (and similarly for later in this century) is not a grand commitment to the generation of peaks of creativity. On the contrary, at all times, in so far as we can judge from this and other admittedly fragmentary evidence, the preponderance of support is for the routine as judged in retrospect and even as given in the perspective of each historical epoch. "Routine" as used by us does not necessarily imply lack of sophistication nor are we equating that term with applied work. What we mean is that the funding is to continue patterns of activities and behavior already in place which may or may not be changing in some significant ways, quantitative or qualitative.

Nor is that necessarily bad from the perspective of intellectual advance. The funding pattern, taken as a whole, reflects two purposes: the maintenance of a culture of "science" or of "research," and the erection of a supporting infrastructure of organizations, social processes, and value judgments furthering the maintenance and growth of that culture. What that indicates to us is that current arguments about R & D funding in the U. S. are couched in traditional terms selected hopefully for their power to convince legislators, administrators, and other dispensers of funds. What is largely absent from such arguments are the real issues: disputes about the nature of the culture of research and disputes about protecting or expanding particular pieces of the infrastructure. What is important from the perspective of intellectual advance as a goal, whatever the specifics at issue, is that now, as in the years 1850–1900, there is general agreement that intellectual advance is important for its own sake and for its possible applied consequences.

Acknowledgments

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NOTES TO TEXT

[1] Reingold, N. 1976. "Definitions and speculations: the professionalization of science in America in the nineteenth century." Pp. 33–69 in *The Pursuit of Knowledge in the Early American Republic . . .* , A. Oleson and S. Brown, eds. Baltimore.

[2] FORMAN, PAUL, JOHN L. HEILBRON, AND SPENCER WEART. 1975. Physics *circa* 1900: Personnel, Funding, and Productivity of the Academic Establishment, vol. 5 of *Historical Studies in the Physical Sciences.* Princeton.

[3] Pfetsch makes a distinction between support for "Imperializing" activities following German unification, "general" support described as "mainly academic and medical," and economically oriented research. To North American eyes "zweck" or mission related research occurs under each category. A notable example of how concentrating on economic results organizes quantitative data bearing on the sciences is PETER LUNDGREEN, *Bildung und Wirtschaftswachstum in Industrialisierungsprozess des 19. Jahrhunderts,* Berlin, 1973.

[4] Carnegie Institution of Washington, *Report of the Executive Committee to Board of Trustees,* Washington, 1902, pp. 247–269.

[5] See: REINGOLD, N. 1978. National style in the sciences: the United States case. Pp. 163–173 in *Human Implications of Scientific Advance,* E. G. Forbes, ed. Edinburgh.

I. COMPARATIVE TABLES

A. 1850*

		USA	UK	REICH	GERMAN STATES
I.	AGRICULTURE AND FISHERIES	18	115	—	106
	A. Agriculture (including Forestry)	18	—		
	B. Botanical Gardens	—	115		
	C. Fisheries	—	—		
II.	GENERAL SCIENCE, TECHNOLOGY	1750	163	—	62
	A. Geophysics (including topographic surveys)	1247	—		
	B. Geology	122	163		22
	C. Meteorology	—	—		
	D. Standards	[8]	—		—
	E. Patents	318	—		—
	F. Other	63	—		40
III.	MEDICINE AND HEALTH	—	205	—	682
IV.	ACADEMIES AND SOCIETIES	—	129	—	252
V.	OTHER SCIENTIFIC ACTIVITIES	—	—	—	385
VI.	MUSEUMS	—	84	—	25
VII.	HIGHER EDUCATION	1	40	—	2507
VIII.	MILITARY	732	111	—	245
	A. *Army*	206	—		
	1. Surveys	153	—		
	2. Education	53	—		
	3. Other	—	—		
	B. *Navy*	526	111		
	1. Hydrography		—		
	2. Astronomy (including nautical instruments)	405	111		
	3. Nautical Almanac	—	—		
	4. Education	63	—		
	5. Other	58	—		
TOTAL		2501	847	—	4264

* All amounts given in 1000's of German marks.

I. Comparative Tables
B. 1860*

		USA	UK	REICH	GERMAN STATES
I.	AGRICULTURE AND FISHERIES	201	552	—	173
	A. Agriculture (including Forestry)	168	—		
	B. Botanical Gardens	33	330		
	C. Fisheries	—	222		
II.	GENERAL SCIENCE, TECHNOLOGY	3225	399	—	143
	A. Geophysics (including topographic surveys)	2236	—		
	B. Geology	—	399		—
	C. Meteorology	—	—		—
	D. Standards	[10]	—		—
	E. Patents	967	—		—
	F. Other	22	—		143
III.	MEDICINE AND HEALTH	3	124	—	759
IV.	ACADEMIES AND SOCIETIES	—	161	—	100
V.	OTHER SCIENTIFIC ACTIVITIES	630	674	—	81
VI.	MUSEUMS	17	641	—	126
VII.	HIGHER EDUCATION	—	257	—	3221
VIII.	MILITARY	1184	1246	—	195
	A. *Army*	691	270		195
	1. Surveys	611	—		
	2. Education	74	239		
	3. Other	6	31		
	B. *Navy*	493	976		
	1. Hydrography		626		
	2. Astronomy (including nautical instruments)	329	222		
	3. Nautical Almanac	69	91		
	4. Education	39	—		
	5. Other	56	37		
TOTAL		5260	4054	—	4798

* All amounts given in 1000's of German marks.

I. Comparative Tables
C. 1870*

		USA	UK	REICH	GERMAN STATES
I.	AGRICULTURE AND FISHERIES	734	1184	—	569
	A. Agriculture (including Forestry)	628	280		
	B. Botanical Gardens	106	515		
	C. Fisheries	—	389		
II.	GENERAL SCIENCE, TECHNOLOGY	4642	3435	33	149
	A. Geophysics (including topographic surveys)	2215	2461		

I. Comparative Tables (*Continued*)
C. 1870*

		USA	UK	REICH	GERMAN STATES
	B. Geology	83	700	—	12
	C. Meteorology	[63]	206	—	
	D. Standards	[18]	—	33	5
	E. Patents	2340	—	—	—
	F. Other	4	68	—	132
III.	MEDICINE AND HEALTH	5	439	—	975
IV.	ACADEMIES AND SOCIETIES	—	37	—	113
V.	OTHER SCIENTIFIC ACTIVITIES	8	126	—	349
VI.	MUSEUMS	17	1030	—	230
VII.	HIGHER EDUCATION	—	409	—	5244
VIII.	MILITARY	1939	1580	744	382
	A. *Army*	1257	402	709	382
	1. Surveys	1084	—		
	2. Education	110	257		
	3. Other	63	145		
	B. *Navy*	682	1178	35	—
	1. Hydrography	173	914		
	2. Astronomy (including nautical instruments)	329	193		
	3. Nautical Almanac	96	50		
	4. Education	84	—		
	5. Other	—	21		
TOTAL		7345	8240	777	8011

* All amounts given in 1000's of German marks.

I. Comparative Tables
D. 1880*

		USA	UK	REICH	GERMAN STATES
I.	AGRICULTURE AND FISHERIES	1,560	1,229	460	1,455
	A. Agriculture (including Forestry)	903	534		
	B. Botanical Gardens	85	395		
	C. Fisheries	572	300		
II.	GENERAL SCIENCE, TECHNOLOGY	5,018	4,384	1,516	679
	A. Geophysics (including topographic surveys)	2,379	2,853		
	B. Geology	448	1,008	—	164
	C. Meteorology	[1,575]	299	—	
	D. Standards	27	33	100	5
	E. Patents	2,118	43	624	—
	F. Other	46	148	792	510
III.	MEDICINE AND HEALTH	960	1,597	128	1,318
IV.	ACADEMIES AND SOCIETIES	—	42	—	281

I. Comparative Tables (*Continued*)
D. 1880*

	USA	UK	REICH	GERMAN STATES
V. OTHER SCIENTIFIC ACTIVITIES	85	38	—	380
VI. MUSEUMS	926	3,820	87	326
VII. HIGHER EDUCATION	10	521	400	14,604
VIII. MILITARY	3,106	1,777	1,553	—
A. *Army*	2,176	294	949	—
1. Surveys	416	—		
2. Education	122	231		
3. Other	1,638	63		
B. *Navy*	930	1,483	604	—
1. Hydrography	251	961		
2. Astronomy (including nautical instruments)	287	274		
3. Nautical Almanac	109	67		
4. Education	90	175		
5. Other	193	6		
TOTAL	11,665	13,408	4,144	19,043

* All amounts given in 1000's of German marks.

I. Comparative Tables
E. 1890*

	USA	UK	REICH	GERMAN STATES
I. AGRICULTURE AND FISHERIES	8,120	1,269	40	1,455
A. Agriculture (including Forestry)	6,718	463		
B. Botanical Gardens	96	429		
C. Fisheries	1,306	377		
II. GENERAL SCIENCE, TECHNOLOGY	9,503	7,164	1,833	1,478
A. Geophysics (including topographic surveys)	1,888	4,445		
B. Geology	3,220	900	—	199
C. Meteorology	[830]	315	—	
D. Standards	16	87	125	5
E. Patents	3,455	1,205	1,159	—
F. Other	924	212	549	1,274
III. MEDICINE AND HEALTH	468	1,294	199	2,505
IV. ACADEMIES AND SOCIETIES	—	119	—	304
V. OTHER SCIENTIFIC ACTIVITIES	43	21	3	1,351
VI. MUSEUMS	757	2,425	63	815
VII. HIGHER EDUCATION	21	1,041	400	18,224
VIII. MILITARY	3,009	1,965	2,294	—
A. *Army*	1,165	398	1,855	—
1. Surveys	14	—		
2. Education	150	93		
3. Other	1,001	305		

I. Comparative Tables (*Continued*)
E. 1890*

	USA	UK	REICH	GERMAN STATES
B. *Navy*	1,844	1,567	439	—
1. Hydrography	408	564		
2. Astronomy (including nautical instruments)	842	344		
3. Nautical Almanac	125	74		
4. Education	105	208		
5. Other	364	377		
TOTAL	21,921	15,298	4,832	26,132

* All amounts given in 1000's of German marks.

I. Comparative Tables
F. 1900*

		USA	UK	REICH	GERMAN STATES
I.	AGRICULTURE AND FISHERIES	13,375	2,100	528	2,452
	A. Agriculture (including Forestry)	11,072	1,154		
	B. Botanical Gardens	109	615		
	C. Fisheries	2,194	331		
II.	GENERAL SCIENCE, TECHNOLOGY	13,874	7,432	3,629	2,519
	A. Geophysics (including topographic surveys)	2,243	4,342		
	B. Geology	2,841	829	{ 3	{ 436
	C. Meteorology	4,157	315		
	D. Standards	44	80	436	8
	E. Patents	4,122	1,405	2,484	—
	F. Other	467	461	706	2,075
III.	MEDICINE AND HEALTH	1,860	1,967	605	2,938
IV.	ACADEMIES AND SOCIETIES	—	152	—	413
V.	OTHER SCIENTIFIC ACTIVITIES	2,409	240	—	3,508
VI.	MUSEUMS	935	2,926	100	1,031
VII.	HIGHER EDUCATION	5,082	2,073	400	27,839
VIII.	MILITARY	2,614	1,978	2,761	—
	A. *Army*	893	180	2,366	—
	1. Surveys	155	—		
	2. Education	189	124		
	3. Other	549	56		
	B. *Navy*	1,721	1,798	394	—
	1. Hydrography	602	740		
	2. Astronomy (including nautical instruments)	359	459		
	3. Nautical Almanac	117	82		
	4. Education	126	154		
	5. Other	517	363		
TOTAL		40,149	18,868	8,023	40,700

* All amounts given in 1000's of German marks.

II. UNITED STATES EXPENDITURES, DETAILED TABULATIONS
(All amounts given in 1000's of German marks.)

	1850	1860	1870	1880	1890	1900
I. AGRICULTURE AND FISHERIES						
A. Patent Office-Agricultural Division[1]	18	168	—	—	—	—
Department of Agriculture[2]	—	—	628	903	6,718	11,072
B. Botanical Gardens[3]	—	33	106	85	96	109
C. Fish Commission[4]	—	—	—	572	1,306	2,194
II. GENERAL SCIENCE, TECHNOLOGY						
A. Coast and Geodetic Survey[5]	987	2,087	2,129	2,350	1,888	2,218
State boundary surveys[6]	—	146	86	29	—	24
International boundary surveys[7]	260	3	—	—	—	—
B. Mineral Land Service	58	—	—	—	—	—
Completing state geological surveys[8]	64	—	—	—	—	—
Geological Survey of Nebraska (Hayden)[9]	—	—	42	—	—	—
Geological Survey (U. S.)[10]	—	—	—	448	3,220	2,721
Mines[11]	—	—	41	—	—	27
Miscellaneous[12]	—	—	—	—	—	93
C. Weather Bureau[13]	—	—	[63]	[1,575]	[830]	4,157
D. Office of Standard Weights & Measures[14]	[8]	[10]	[18]	27	16	44
E. Patent Office[15]	318	967	2,340	2,118	3,455	4,122
F. Exploring Expedition (Wilkes)[16]	63	22	—	—	—	—
Smithsonian—International Exchange	—	—	—	—	63	99
Smithsonian—National Zoological Park[17]	—	—	—	—	861	265
Smithsonian—Astrophysical Observatory	—	—	—	—	—	38
Other Smithsonian[18]	—	—	—	46	—	12
Miscellaneous[19]	—	—	4	—	—	54
III. MEDICINE AND HEALTH						
Vaccination of Indians	—	3	5	1	1	5
District of Columbia—Health Department[20]	—	—	—	101	203	493
National Board of Health[21]	—	—	—	858	—	—
Preventing spread of epidemic diseases[22]	—	—	—	—	217	1,315
Marine Hospital Serv.—Hygienic Laboratory[23]	—	—	—	—	47*	47*

TABLE II (*Continued*)
II. UNITED STATES EXPENDITURES, DETAILED TABULATIONS
(All amounts given in 1000's of German marks.)

	1850	1860	1870	1880	1890	1900
IV. ACADEMIES AND SOCIETIES	—	—	—	—	—	—
V. OTHER SCIENTIFIC ACTIVITIES						
International boundary survey commissions[24]	—	630	8	—	—	63
Panama Canal survey	—	—	—	—	—	2,326
International Bureau of Weights & Measures	—	—	—	8	27	14
International Geodetic Association	—	—	—	—	—	6
Berlin Fishery Exhibition	—	—	—	77	—	—
International Conference for the Protection of Industrial Property	—	—	—	—	17	—
VI. MUSEUMS						
National Museum[25]	—	17	17	926	757	935
VII. HIGHER EDUCATION						
Howard University—science	—	—	—	10*	21*	42*
Colleges for Agriculture and Mechanic Arts	—	—	—	—	—	5,040
Miscellaneous[26]	1	—	—	—	—	—
VIII. MILITARY						
A. *Army*						
1. Surveys for military defenses[27]	6	234	594	—	—	—
Geological Exploration of the Fortieth Parallel (King)[28]	—	—	[168]	—	—	—
Geographical Surveys West of 100th Meridian (Wheeler)[29]	—	—	—	59	—	—
Survey of northern and northwestern lakes[30]	67	377	456	357	14	155
Other surveys[31]	80	—	34	—	—	—
2. Military Academy—scientific staff	53	74	110	122	150	189
3. Engineer's depot, Willet's Point, NY[32]	—	—	—	21	67	41
Signal Corps—Meteorology[33]	—	—	63	1,575	830	—
Ordnance Experiments[34]	—	6	—	—	40	439
Army Medical Museum	—	—	—	42	21	27
Surgeon-General's Office—Library	—	—	—		43	42
B. *Navy*						
1. Hydrographic Office[35]	405	254	173	251	408	602

2. Naval Observatory			229	235	823	339
Nautical Instruments[36]	[42]	68	100	50	—	—
Other Astronomy[37]	—	7	—	2	19	20
3. Nautical Almanac[38]	—	69	96	109	125	117
4. Naval Academy—science[39]	63*	39*	84*	90*	105*	126*
5. Meteorology[40]	5	5	—	—	—	—
Surveys[41]	1	16	—	—	46	211
Torpedo Corps[42]	—	—	—	193	296	283
Other Ordnance and Steam Engineering Experiments[43]	52	33	—	—	22	23
Miscellaneous[44]	—	2	—	—	—	—

* Estimate.

[1] The forerunner of the U. S. Department of Agriculture, the Patent Office's Agricultural Division was, from its inception in 1839, the center of agricultural science in the Government. In 1862, the work of the division was transferred to the newly created Department of Agriculture.

[2] Unlike its counterpart in the twentieth century, with its heavy emphasis on economic planning and rural living conditions, the nineteenth century Department of Agriculture was primarily a center for the promotion of agricultural science and related fields. By the end of the century, its steadily expanding range of activities included research in biology, botany, chemistry, zoology and entymology; veterinary medicine and meat inspection; forestry; nutrition; soil and irrigation studies; and the purchase and distribution of seeds. Because its orientation in this period was overwhelmingly scientific, the entire budget of the Department has been included, except that for 1900 the expenses of the Weather Bureau, which though under the Department of Agriculture was largely self-contained, have been separated out and placed under General Science and Technology—Meteorology.

[3] Though a private botanical garden, under the sponsorship of the Columbian Institute, had previously existed at the foot of the Capitol with Congressional sanction, the first direct appropriation for a national Botanical Garden came in May, 1850, when Congress authorized the construction of a facility to house the plants of the Wilkes Expedition on the site of the by then defunct Columbian Institute garden. The first actual expenditures for this purpose appear in fiscal 1851.

[4] The United States Fish Commission was established by Congress in 1871 for the investigation and promotion of American fisheries. It conducted substantial research in icthyology and marine biology.

[5] The survey of the coasts of the United States was first authorized by Congress in 1807, but the Coast Survey was not actually organized until 1816. In 1818, however, Congress repealed its original authorization, and the Coast Survey was dissolved, although some of its activities were continued in a piecemeal fashion by the War and Navy Departments. In 1832, Congress reestablished the Coast Survey in the Treasury Department, where it remained until its transfer to the Commerce Department at the beginning of this century, save for the period 1834–1836, when it was under the supervision of the Navy Department. In 1878, it was renamed the Coast and Geodetic Survey in recognition of the geodetic activities with which it had been charged by Congress in 1871. Though its activities ranged to include—in addition to its topographic, hydrographic, and geodetic surveying operations—astronomy, oceanography (primarily tide studies), terrestrial magnetism, seismology, gravitation, and even a little meteorology, the great preponderance of its activities may be subsumed under the general heading Geophysics.

[6] 1860—Minnesota boundary, Texas boundary.
1870—California-Oregon boundary, Nebraska boundary. Nebraska-Colorado boundary.
1880—Colorado-Utah boundary.
1900—Idaho-Montana boundary, Locating the 98th meridian.

[7] 1850—U. S.-Mexico boundary, U. S.-British provinces northeastern boundary.
1860—U. S.-Mexico boundary.

[8] Listed in expenditures as "Completing geological surveys of Michigan, Wisconsin, etc."

TABLE II (*Continued*)

[9] The U. S. Geological and Geographical Survey of the Territories, or Hayden Survey, under the direction of geologist F. V. Hayden, originated in a Congressional appropriation in 1867 for the geological survey of Nebraska, by which label it is still identified in the 1870 expenditures. Although the survey included work in natural history, ethnology and topography, along with its strictly geological activities, it has been included under Geology because (1) its mission was primarily geological and (2) it was a direct antecedent of the U. S. Geological Survey, under which it was subsumed when the latter came into existence in 1879.

[10] The U. S. Geological Survey was established in 1879 by the merger and expansion of the Geological and Geographical Survey of the Territories (Hayden) and the Geographical and Geological Surveys of the Rocky Mountain Region (Powell), both under the Interior Department, and the Geographical Surveys West of the 100th Meridian (Wheeler), under the War Department. A fourth survey, the Geological Exploration of the Fortieth Parallel (King), was also antecedent to the creation of the U. S. Geological Survey, though it had actually terminated its work a year earlier. For Hayden Survey, see footnote 9. For King Survey, see footnote 28. For Wheeler Survey, see footnote 29. The Powell Survey, which was active from 1874 to 1879 does not appear in the expenditures for either 1870 or 1880.

[11] 1870—"Collecting reliable statistical information concering the gold and silver mines of the western States and Territories".

1900—Inspecting mines in the Territories.

[12] 1900—"Examinations of desert lands," "Classification of certain mineral lands in Montana and Idaho"

[13] The first full-time large scale weather service was established in the Signal Corps of the U. S. Army in 1870. The expenditures for this establishment are therefore included under Military science, although for convenience they have also been shown under General Science and Technology—Meteorology, but in brackets to indicate that they have already been included elsewhere. In 1891, in recognition of the importance of reliable weather forecasting to farmers, a new Weather Bureau was established in the Department of Agriculture, and the meteorological work of the Signal Corps transferred to it. Prior to 1870, some meteorological observations had been conducted by a variety of Government departments, including the Hydrographic Office of the Navy (see Navy—Meteorology), the Medical and Engineering Departments of the Army, and the General Land Office. The largest meteorological establishment prior to 1870, however, was under the direction of the Smithsonian Institution, which in 1860 spent 19,000 M to support its network of weather observations. But the Smithsonian's meteorological work was supported from the Institution's endowment income, not Congressional appropriations, and thus cannot be counted as Government science. In 1873, the meteorological activities of the Institution were transferred to the Signal Corps.

[14] Although an office of standard weights and measures was established in the Coast Survey in 1830, the first specific line appropriation for this purpose appears in 1873. The figures in brackets for 1850, 1860, and 1870, therefore, represent funds which are included in the general Coast Survey expenditures, but which it has been possible to identify as being devoted to salaries for the Survey's weights and measures activities. Again, the brackets are used to indicate that this is the second time that this money has appeared, and so to avoid the danger of duplication in the totals. In 1891, the office was officially designated the Office of Standard Weights and Measures, which it remained until 1901 when it was removed from the Coast and Geodetic Survey and renamed the National Bureau of Standards.

[15] Although, in general, capital expenditures on buildings for scientific organizations have been included in the estimates of expenditures, in the case of the Patent Office Building an exception has been made. In contrast to the buildings for the Botanic Gardens, Naval Observatory, or National Museum, for example, where relatively modest facilities were constructed specifically suited to the needs of the institution, the Patent Building was one of the most imposing structures in Washington and bore little relation, if any, to the activities it housed. For this reason, it was thought undesirable to inflate the expenditures of the Patent Office by including these building costs, and they have therefore been deleted from the totals for the years where it is relevant, namely 1850, 1860, and 1870.

For 1850 and 1860, the expenses of the Patent Office's Agricultural Division have been separated out and placed under Agriculture.

[16] Though the Navy's Exploring Expedition, under the direction of Lieutenant Charles Wilkes, was confined to the period 1838–1842, follow-up work, in the form of reports, preservation of collections, etc., continued for many years, and it was for this purpose that the expenditures listed for 1850 and 1860 were made.

[17] The National Zoological Park was authorized by Congress in 1889. The unusually large expenditures for 1890 presumably reflect the high initial capital costs connected with its establishment.

[18] 1880—Smithsonian: Polaris report; Smithsonian: protection against fire.

1900—Smithsonian: Solar eclipse observations.

Here, and previously, only federal funds are reported. The Smithsonian's private funds are omitted; these represented the bulk of expenditures in the earlier years, but were increasingly overshadowed by official appropriations. The federally-funded Bureau of American Ethnology has also been omitted because it does not meet the definition of "science" that we have employed based on the categories in the British and German compilations. In general work in the social sciences (*e.g.,* the Census) is omitted.

[19] 1870—Light-House Board experiment.
1900—Introduction of Reindeer to Alaska.

[20] The District of Columbia Health Department has been included on the basis of its similarity to the Local Government Health Board in the British estimates.

[21] The National Board of Health was established in 1879 in response to the yellow fever epidemic of 1878. It ceased operations in 1886.

[22] Although administered by the Marine Hospital Service, these funds were appropriated separately. While the budget of the Marine Hospital Service has not been included in our list of expenditures because it was primarily devoted to the maintenance of marine hospitals and coastal quarantine stations, the funds included under this appropriation were intended for more general public health considerations throughout the country, and in some ways may be regarded as a continuation of the expanded public health activities generated by the National Board of Health. In 1902, the Marine Hospital Service, which had first been established in 1798, became the Marine Hospital and Public Health Service, and in 1912 its name was shortened to the Public Health Service.

[23] The Hygienic Laboratory was the unit of the Marine Hospital Service devoted to basic medical research, and has therefore been included in this list of expenditures even though the rest of the Marine Hospital establishment has not. The Hygienic Laboratory was established in 1887 at the Marine Hospital on Staten Island, New York, and was transferred to Washington, DC in 1891. The figures shown here are only minimum estimates, and include only salaries. The actual expenses of the Laboratory were undoubtedly larger, but we have been unable to isolate them from the overall Marine Hospital Service Budget. Although occurring too late for the 1900 estimate, Congress did, in 1901, appropriate 147,000 M for the construction of a new facility for the Laboratory.

[24] 1860—Northwestern Boundary Commission (1857–1861), to determine, in conjunction with its British counterpart, the boundary between American and British possessions in Washington Territory.
1870—Northwestern Boundary Commission followup.
1900—International Commission: Mexican boundary survey (1882–1896) followup; Mexican Water Boundary Commission (1889–post 1900).
These boundary surveys, unlike those included under Geophysics—International boundary surveys, were not solely American operations, but were supervised by joint international commissions, and were funded through appropriations for "Foreign Intercourse." Therefore, they have been included with other international activities and special commissions under Other Scientific Activities.

[25] While the National Museum had been one of the responsibilities assigned to the Smithsonian Institution at its inception in 1846, it had initially been funded out of the Institution's private income. The first federal appropriation for this purpose came in 1858, in the form of 17,000 M for the preservation of the collections of the exploring expeditions of the Government, with which the Smithsonian had been charged. This standard 17,000 M appropriation continued for many years at the same level, and then began to be rapidly increased as the activities of the National Museum expanded. The figure for 1880 is unusually high because it includes 798,000 M for the construction of the new building for the National Museum which was underway at the time.

[26] 1850—"Refunding duties on philosophical apparatus to colleges, seminaries, etc."

[27] This was the general rubric used by the Army to include a variety of scientific surveys and investigations conducted by the Corps of Topographical Engineers. The figure for 1870 includes 168,000 M for the King Survey, (see footnote 28) as well as funding for the initial stages of the Wheeler Survey (see footnote 29).

[28] The Geological Exploration of the Fortieth Parallel, under the direction of geologist Clarence King, originated in 1867 and continued until 1878. Along with the Hayden, Powell, and Wheeler Surveys, it formed the foundation for the U. S. Geological Survey. The brackets indicate that the expenditures have already been included under Surveys for Military Defenses.

[29] The Geographical Surveys West of the 100th Meridian, under the direction of George M. Wheeler, originated in 1869, although were not officially designated as such until 1872. For this reason, no expenditures appear for 1870, but are subsumed under the general appropriation for Surveys for military defenses. Although the field work of the survey was transferred to the U. S. Geological Survey in 1879, the office work, in the form of drafting reports, etc., continued until 1884, and it is this activity that is represented by the figure for 1880.

TABLE II (*Continued*)

[30] The survey of northern and northwestern lakes originated in 1841. The field work was terminated in 1882, but was resumed again at a reduced level in 1889, although the office work continued through this hiatus. The survey conducted astronomical, meteorological, topographic, hydrographic, and geodetic observations throughout the Great Lakes region.

[31] 1850—Pacific coast examinations, Surveys of routes from Mississippi to Pacific, Surveys with armies in the field.
1870—Surveying Isthmus of Darien for ship canal.

[32] The Engineer's Depot at Willets's Point was the center of scientific instruction and experimentation for the Corps of Engineers.

[33] See footnote 13.

[34] 1850—Testing gun metal.
1890—Testing machine (Watertown Arsenal).
1900—Testing machine (Watertown Arsenal); Board of Ordnance and Fortification.
The figures for ordnance are minimums, based only on what can be derived from line item expenditures or appropriations. A considerable amount of ordnance experimentation was conducted within the Ordnance Department, but we have been unable to isolate the expenditures devoted to these purposes. Based on the Annual Report of the Secretary of War (1880), the testing machine at Watertown Arsenal (Massachusetts), used to test metals, was one of the preeminent experimental facilities in the Army, and was used by civilian as well as military science. The Board of Ordnance and Fortification, charged with the planning and supervision of experiments, though in existence prior to 1900, does not appear as a separate line item in any of our earlier sample years. The expenses of the proving ground at Sandy Hook, New Jersey, though they appear in both the 1890 and 1900 accounts (115,000 M in 1890; 262,000 M in 1900) have not been included because it was engaged in weapons firing tests that can only be considered marginally scientific.

The basic difficulty in trying to arrive at accurate figures for science within military ordnance during this period is the inability to separate the budget for experimental purposes from the overall ordnance budget, the great preponderance of which was devoted to the procurement and manufacture of weapons and ammunition. While the Annual Reports of the War Department are filled with records of experiments, there is no account of expenses accompanying them whatsoever. Therefore, while appropriations for certain specific purposes are occasionally listed separately, much of the ongoing research activity is lost within the huge budget for the general ordnance establishment. In general, as the century progressed, there was a tendency to enumerate more of the component parts of the Department. For this reason, the dramatically increased spending shown for ordnance experiments in 1900 is attributable only partly to increased activity; a large fraction is due simply to the fact that the Board of Ordnance and Fortifications for the first time appears as a separate line item, and can therefore be included.

One must conclude, therefore, that the expenditures shown for ordnance experiments and research are seriously underrepresentative. The British figures for these purposes are also quite small, suggesting the same difficulty.

[35] Until 1866, the Naval Observatory and Hydrographic Office was a single unit, and the expenditures on both are therefore combined. The unusually large figure for the Naval Observatory in 1890 includes a capital expenditure of 590,000 M for a new facility.

[36] For 1850, the bracketed figure indicates that the expenses on nautical instruments have already been included in the budget for the Naval Observatory and Hydrographic Office. For 1890 and 1900, the expenses on nautical instruments are included in the budget for the Naval Observatory.

[37] 1860—Naval astronomical expedition.
1880—Observation: transit of Mercury; Observation: solar eclipse; Velocity of Light.
1890—Observation: solar eclipse.
1900—Observation: solar eclipse.

[38] Although work on the preparation of an American Nautical Almanac had begun earlier, the first expenditures for this purpose do not appear in the accounts until 1851, too late for our estimates for 1850.

[39] These figures are estimates based on salaries and incidental expenses.

[40] See footnote 13.

[41] 1850—Survey of coast.
1860—Exploration of Paraguay; Darien Isthmus Survey; Surveying and Exploring Expedition.
1890—Ocean Surveys.
1900—Ocean and lake surveys.

[42] The torpedo station at Newport, Rhode Island, was the Navy's center of instruction and experimentation in torpedoes, and was first funded in 1871.

[43] 1850—Testing steam boiler explosions; "Testing Prof. Page's electromagnetic power."
1860—Testing steam boilers; testing useful inventions and discoveries.
1890—Testing American armor; testing Clark's deflective turret.
1900—Experiments with armor-piercing projectiles; Experiments with liquid fuel.

To some extent, we encounter the same difficulties here that we do in Army ordnance, except that in the case of the Navy two bureaus, those of Ordnance and (from 1862) of Steam Engineering, were engaged in experimental work. On the other hand, the accounts of expenditures which appear in the Annual Reports of the Navy Department are more detailed than those of the War Department, and in many cases include a separate line entry labeled "For experimental purposes." In a number of instances (for example, Ordnance in 1870, and Steam Engineering in 1890), the amount listed as spent on experimentation is zero, suggesting that the low figures we report for some years may not be so unrepresentative after all. Even in these cases, however, one suspects that some experimental work continued, if under another guise.

[44] 1860—listed simply as "Arranging, etc., specimens of natural history."

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LAYING THE GHOST: EMBRYONIC DEVELOPMENT, IN PLAIN WORDS

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—Met him what? he asked.
—Here, she said. What does that mean?
—He leaned downward and read near her polished thumbnail.
—Metempsychosis?
—Yes. Who's he when he's at home?
—Metempsychosis, he said, frowning. It's Greek: from the Greek. That means the transmigration of souls.
—O rocks! she said. Tell us in plain words.

—James Joyce, *Ulysses*. II.

Creative Ghosts[1,2]

The battle between Preformationism and Epigenesis is more than its recurrent skirmishes on the field of embryology. It is among the oldest of philosophical battles. In the seventeenth century, Thomas Hobbes, from whom a materialist, epigeneticist position might have been expected,[3] nevertheless made the pure preformationist case, in plain words: "Nothing taketh a beginning from itself." (The epigeneticist response could have been: "Creation occurs; complexity obviously arises from simplicity.") On this issue philosophers and scientists have spoken inconsistently more often than on most others, and great biologists have been no exception.

Epigenetics of the nineteenth century, when the Stazione Zoologica in Naples was a beacon and the MBL in Woods Hole was gathering strength, did not require Creation to follow Archbishop Ussher's scenario—the world established by successive strokes of God a few thousand years earlier. It could be more subtle. Moreover, questions of meaning and "explanation" were in the air, and there was an exhilaration with change. Lecturing to the MBL community in 1895 on mind and matter, A. E. Dolbear said:

> . . . the past thirty years shows that in the field of natural history everybody has changed from a creationist to an evolutionist. But this has been only the beginning of the change, for if that science was true that made such a change necessary, it is also true that the same science will make needful other changes in men's conceptions of what kind of a universe they live in, how it works, and how they came to be and think as they do; and not unlikely that what we please to call evolution will have to be explained and restated in very different terms than those in vogue now.[4]

So spoke Dolbear of Tufts College, and he could with confidence dismiss all antecedent theology and metaphysics as irrelevant, specifically to the issue of origins. But then in the end he, too, foundered on the seeming plain sense of preformation: you can't get something from nothing. In the end he argued that the *universal ether*, at least, must have been created. Having first laid to rest an earlier ghost, he raised a different one. The battle continues, as it has since then—if not since Aristotle—with the forms of argument changing as the foci of scientific theory change. By the nineteenth century, serious fighting about the origins of complexity had fallen to science, and there it remains. Like all arguments of principle and common sense, it

is fought not just with reason, mathematics, observation, or measurement: but sometimes with feelings, alliances, power, and politics, with all the trappings of society and culture, which some contemporary historians insist are the primary drives of scientific inquiry, rather than a subset of them. I reject the insistence; but that the trappings are there is undeniable.

Preformationism *versus* Epigenesis is not merely a diversion for embryologists; nor for cosmologists. It is difficult for a sober mind to imagine how order might arise from disorder, long-range structure from randomness. The discoveries of nineteenth century physics, especially of thermodynamics, put an end to the most primitive possibility—that organized macroscopic structure may appear *spontaneously* in a structureless or truly homogeneous system. In the absence of appropriate work done from the outside, this does not happen.[5] But embryologists of the late nineteenth century and early twentieth, although many were impressed by the power of physics, seem not to have been overly concerned with thermodynamics. And in modern physics the issue becomes clouded again, at least in the sense that a vacuum is no longer what we had thought it to be: in the quantum universe material particles can and do arise spontaneously; not from "nothing," but because it is necessary to re-define "nothing."[6]

The Mind in the Embryo

The search for an explanation of development—that most awe-inspiring of all processes of the biological world, in which a complex and functional being emerges from a zygote that is seemingly structureless under the microscope—has included a long succession of creative ghosts. Those have been the agencies or blueprints by which the form of the embryo and adult is built. They have changed in character from the ridiculous—the homunculi of ovists and animalculists in the seventeenth and eighteenth centuries—to the sublime—the originally naked and self-replicating polynucleotide, from which everything else takes its guidance and form. But the effort to exorcise the ghosts, material or immaterial, continues nevertheless, and not only from the embryo: from an anthropic cosmos no less than from consciousness (whose ghost is an entity called "mind").

Toward the turn of the last century, before the Proud Tower of Europe began to lean,[7] but when the strains were already felt and influential in the styles of scientists, the ghost in the embryo assumed a new and unexpected form. For obscure and to some extent accidental reasons, the creative ghost became, under the influence of Haeckel, the old *Scala Naturae* in a new dress: the embryo retracing faithfully and by necessity the evolution of its ancestors. The inevitable opposition, when it arose, did not so much refute the broad claim (although it *was* refuted in detail) as bypass it and deem it irrelevant. This reaction began in Europe, notably with Wilhelm His, but the arguments were heaviest and most influential among others, at the Stazione Zoologica; curiously so, given the commitment of the founder, Anton Dohrn, to Haeckel's genealogical apparition. By this time, there were able young Americans who could commit themselves fully to fundamental research in biology. Those who later became founders of the Marine Biological Laboratory in Woods Hole were aware of, and later in the thick of, the Naples arguments. They did not fail to carry them to Woods Hole. The concentration of intellect and skills at the MBL led to newer and more powerful arguments; to important discoveries of observation and experiment; and in the end to laying to rest the ghost, for at least the interval from then until now.

Whether it has been exorcised for good I do not venture to guess; but allow me my doubts. Mind/Brain dualism remains in good health, even among respectable psychologists; and as it becomes clear to most biologists that there are not enough genes to specify all the connections, *one by one,* among neural elements, let alone the emergent operating systems of the brain, the ghost may walk again. This too is, after all, a problem of biological development. In any case, the foundations of several branches of modern biology were laid in the course of early embryological arguments at Woods Hole, not the least of those branches being experimental embryology, general physiology in the new forms that led to what we now identify as "cell biology" and "biophysics," and modern genetics. It is a tangled story which needs still-unwritten books in order to be told properly.

Haeckel's Synthesis

Ernst Heinrich Haeckel grew up in the conservative atmosphere appropriate to his father's position as a higher civil servant (*Regierungsrat*) in the best Prussian mold. Haeckel was a gifted student and studied under the best teachers: botany under Schleiden (Jena); anatomy and physiology at Würzburg under Kölliker; pathology under Virchow; and physiology under J. Müller in Berlin, where he acquired his devotion to marine research. He published an important work of comparative morphology, *Die Radiolarien,* after extensive marine collections at Messina, and became Professor of Zoology at Jena in 1862, where he remained until 1909. Afterward he continued writing until his death, at the age of 75, in 1919.

It was a life full and productive, and enormously influential. The influence upon embryology was one among many, but the embryological one lasted longer than did the others. This influence owed much to the particular ingenuity with which Haeckel made an unique amalgam of the three great but disparate influences on his own thought: Darwin, Goethe, and Lamarck. How this unlikely Trinity came to be is in essence simple, but the essence does poor justice to Haeckel's energy in applying it to a whole system of thought about life on earth, and in triumphing, by polemic, over its many detractors.

Haeckel was for a long time a good boy; conscientious, devoted to his parents and their ideals, such as German unification. Right-thinking came easily to him. Thus, Nordenskiöld, referring to Haeckel's letters written when he was away from home:[8]

> True, he could cause his parents anxiety on account of his dislike for medicine and his propensity for unpractical dreaming, but, on the other hand, he was always ready, with a somewhat rhetorical and precocious eloquence, to confess his weaknesses to his old parents and to promise to make them happy in the future. The most striking feature of these letters is their Christian piety, which contrasts strongly with the hatred that Haeckel felt for Christianity in later years. . . .

He was for a time an ardent German nationalist, and a passionate denouncer of Germany's enemies, within and without.[9] But he was also an observer. The enthusiast of twenty-five became a skeptic at thirty-five. A new, imperial Germany did *not* broaden the rights of man, nor loosen the bonds of religion allied with reactionary elements of the state; quite the reverse. Freedom of thought, which is important to professors, did *not* increase with material progress and national power: it was decreased, often brutally so. Haeckel made early the discovery that noble

thoughts, translated into political reality, do not necessarily pass directly into good actions. They are just as likely to pass to the reverse.

All the while, his professional work, molded strongly by the standards of Würzburg (where Karl Gegenbaur now held sway), was devoted to the good German purpose of creating a *weltanschauung*, a worldview and an ordered system, through which living nature, and man within it, might be fully comprehended under a liberal ideal of progress. The central tool for its construction, as already established by Gegenbaur and others, would be comparative morphology; the structure, an objective and self-consistent phylogeny, which would explain what and why the living world is as it is, and in what directions it would go.

Disappointed in his hopes for reform and progress in the spheres of politics and general culture, he fashioned a system of thought within his professional discipline that would substitute; that would, at one and the same time, deny the significance of princes, politicians, and the priests who supported them in oppression, and hold out to mankind a vision of harmony and progressive change in the forms and conditions of life. He found within his experience three guides. The first was Darwinism, enthusiasm for which, in the form of comparative morphology, he had already acquired as a student and a correspondent with, and collaborator of, Gegenbauer.[10] It was the evidence of common descent that gave Haeckel the key to his *weltanschauung*. Common descent immediately defies special creation: thus it defied the establishment; common descent bespeaks flux, change, relatedness among all things living, and by a very small (and then still allowable) step, it implies progressiveness. The second guide was Goethe. It was not merely that the poet and polymath of Weimar had been a natural philosopher, the definer of "morphology," but that he had been a champion of evolution before Darwin. He had also, however, been an honored Minister of State in liberal Weimar. He had rhapsodized change and gotten away with it. And withal, Goethe had lived to a ripe old age: a survivor, with authority. This example before him, Haeckel, who insisted upon the importance of a *mechanical* basis for his new system, took on in fact Goethe's unmechanical, romantic idealism, in a form that had already been expunged from the physical sciences and from physiology.[11]

And finally Lamarck; to whom Haeckel gave credit for having understood the *mechanism* of living transformations over time, whereas Darwin he seems to have credited as more or less the demonstrator of their occurrence. Throughout the whole ran that strong tendency of the time toward viewing history as the determiner of events—a tendency in no way limited to biology: a description of how things had come about was accepted as the explanation of why things are as they are.

Haeckel's greatest work was the *Generelle Morphologie*, published in 1866, with its latter and most important part modestly dedicated to Darwin, Goethe, and Lamarck. For embryology, however, it is not this impressive tome, but the later *Anthropogenie oder Entwicklungsgeschichte des Menschen* (1874) that was to be determining for decades to come. This book had no less a purpose than a complete description of the biological origins of the human race, as reconstructed from the facts of paleontology, embryology, and comparative anatomy.

In it Haeckel presents fully-formed what came to be called the "Biogenetic Law," *i.e.*, that "ontogeny is a brief and rapid recapitulation of phylogeny." The general idea was not new: it had been proposed earlier by others, including, notably, Meckel and Fritz Müller; but in Haeckel's hands it becomes the motto and the program for biological research, especially in embryology. The purpose of embryology is to trace out genealogy—to identify, by means of close observation of embryonic form, the details of phylogenetic relationships among animals, the history of their

descent. The history will be the explanation; for the *fact* of organic evolution is not in doubt, and its mechanisms seem close to being known. For this program of embryological research there was ready to hand a most fortunate tool: the morphogenesis of germ layers, whose universal homology seemed to Haeckel perfectly obvious.

The facts of embryonic development, in short, he saw as the strongest support of common descent, and at the same time the still unexplored territory by which its details—hence the detailed history of life—are to be wrested from nature. The germ layers arise at gastrulation: hence the development of form *after* that stage of embryogenesis is to be studied. From such studies are to be reconstructed the genealogies that will establish not only the tree of life, but also the sap flowing in it. For twenty-five or thirty years this program was the preoccupation of embryology, which was in turn perceived as the strong right arm of general morphology, and, of course, of Darwinism. Haeckel, exorcising the ghost of special creation from embryonic development, substituted another one: phylogeny as the directing intelligence, phylogeny not merely the result, but the *mechanical cause* of development. (Why bother, then, with physiology, or with cleavage, which was a mere subdivision of the bulky egg into better-deployable, small units?[12])

Reaction was not slow in developing, although thirty years were required for it to affect the work of most biologists. Haeckel gathered round himself a group of enthusiastic followers, many of whom associated themselves willingly with a political radicalism they conceived as matching their scientific stance. But not expectedly, for every accomplished scientist who espoused the radical program entire, there was an equally distinguished one who, for reasons of his own, opposed it. The first attacks upon Haeckel had other than purely scientific motives. For example: Haeckel's system included (naturally) a program for educational reform: this was attacked by no less a figure than Haeckel's former teacher, Rudolf Virchow, who in so doing placed himself in the uncharacteristic position of arguing that the teaching of *hypotheses* should be banned.

These arguments, emotional as they were, attracted less attention than desired by their proponents. Militarists and socialists had other fish to fry; and the arguments of zoologists were in any case incomprehensible to most policy-makers, let alone to the masses. Haeckel's program for embryological and morphological research survived such arguments by many years, as it did the other philosophical quarrels that marked the death-throes of natural philosophy. The destruction of Haeckelian embryology came from another quarter entirely: that of cytology, with its remarkable discoveries of cell structure, growth, and division (Strasburger's monumental *Zellbildung und Zelltheilung* was published in 1874 and became truly influential a decade later); of fertilization and its early consequences (Fol, 1879); and from the new *experimental, i.e.,* manipulative and invasive, embryology, championed by Wilhelm His, by Roux, Boveri, the Hertwigs, and in the end by a whole school of Naples investigators whose most aggressive—and abrasive—voice was that of Hans Driesch.

The reaction at Naples is critical to the unfolding story of Haeckel's overthrow and the rise of modern embryology; but I shall not address it here. It is the subject of a chapter elsewhere in this volume. Suffice it to say that the Americans were aware of it and involved in it, and that without such involvement the MBL would not have come to be what it is. American biology would have been something less. The MBL story, insofar as it can be represented here, must begin not with outspoken anti-phylogenesis—for that came later—but with the transitional work of its remarkable founding Director, Charles Otis Whitman.

Whitman Spurs, and Controls, the Revolution in America

If Haeckel caused a revolution in embryology, then the mechanist-experimental wave was its counter-revolution. Whitman helped, despite himself, to bring it about, by demonstrating the power and value of cell lineage research; and yet he was able to control the inevitable after-shocks (which included a rejection even of cell lineage) by the power of persuasion, by the breadth of his mind, and by his skill as a scientific administrator. It is true that the name "cell lineage" was applied first by E. B. Wilson to "the study of the cell-by-cell origin of body regions and organs characteristic of the development of annelids, most mollusks, many crustacea, the tunicates, and a few other animals, in which the cleavage of the egg is determinate."[13] But Whitman must be counted among the actual inventors of the methodology, the first to demonstrate its power.

Writing in *The Proud Tower* of Thomas B. Reed, Republican of Maine and elected speaker of the U. S. House of Representatives in 1890, Barbara Tuchman uses words that might apply equally well to the contemporary Whitman:

> . . . in character, intellect and a kind of brutal independence . . . (he) . . . represented the best that America could put into politics in his time. He was sprung from a rib of that hard northern corner of New England with the uncompromising monosyllabic name. . . . The sons of Portland families went to Bowdoin, not to satisfy social custom, but to gain a serious education.

So too Maine-born Whitman, who studied the classics at Bowdoin, displayed throughout his life a certain brutal independence, supported by an agile intellect and an unwillingness to submit to authority unless its sources had survived his own examination. The United States had neither a landed aristocracy nor an intellectual one, except for the small cluster of thinkers who survived in the vicinity of Boston. Those did not exert much influence upon the culture outside a few universities. The nation was a German liberal's dream come true: abdication of the rich from politics; government loose, flexible, manipulable—and self-serving; growth in wealth and power but without the restrictions of landed inheritance and hereditary privilege; the poor under control. A capitalist's heaven, and one in which as much honor was given to financial achievers (even if achievement was by dubious means) as was denied to politicians.

To be sure, not all was peace and tranquility. Healing the Civil War's wounds was the healing of a large adolescent, growing like a weed, feeling the desires of adolescence. The inevitable conflict erupted in the Spanish-American war of 1898—a conflict between those hungry to use their strength to seize external riches, and those who saw in the emulation of European imperialism the death of the American social ideal. Leading the former were those two "degenerate sons of Harvard" (as Harvard's President Eliot named them), Theodore Roosevelt and Senator Lodge, supported by the popular press; and leading *conscience* were a few of the Bostonians (including the same Eliot), a few journalists, and some honest politicans (including Reed). Conscience lost and Jingoism won. But the Caribbean, and more so the Pacific islands, were sufficiently remote from the great land between two oceans so that they had small effect. It was an expanding and confident society, unencumbered by ancient power-structure and innocent, after Appomattox, of war on its own soil. Able men of conscience who did politics did it, and were lonely. Able men of science or the arts did those; and they did not bother much about politics.

Like Thomas Reed, Whitman became a school-teacher upon graduation from Bowdoin: at age twenty-six he became principal of the Westford Academy in

Westford, Massachusetts; and in 1872, at the age of thirty, he joined the faculty of the English High School in Boston. It was here that his interest turned to natural history. He attended the two sessions of Louis Agassiz's Anderson School on Penikese Island in 1873 and 1874. In 1875, having decided to stake his future upon a career in science, he did what it was necessary to do in order to obtain the best training: he sailed for Germany with the intention of studying natural history and earning a doctorate there (in the laboratory of Rudolf Leuckart, at Leipzig). In 1878, a man no longer young to be starting in science, he received the doctorate and published a dissertation on the embryology of leeches of the genus *Clepsine*.[14]

Just as Whitman himself emerged as an unique transitional figure in scientific thought and administration in America—aware of all that was new, and receptive to it, but unwilling to sacrifice the values of the old simply for the sake of novelty—so, too, is this hundred-page memoir of Whitman's transitional. Its length was not unusual at the time, nor for some time longer: witness the extraordinary length and detail of monographic papers published by such followers of Whitman as Wilson and Conklin. Nor is there any direct or obvious rejection of the genealogical concerns that so characterized contemporary works of embryology or comparative morphology. It is simply that these concerns are, in Whitman's work, *mere obeisances,* by comparison with the extraordinary detail and attention devoted to the three central sections. These deal, in order, with the cytology of maturation and of the uncleaved zygote—employing every sophistication of method recently introduced by the cytologists ("*die aniline-färber,*" of whom other embryologists were scornful); with an exact description of cleavage itself and of the fates of blastomeres; and finally with the morphogenetic movements of gastrulation and neurulation, which—despite Whitman's delicacy in not making a great point of it—threw doubt upon the prevailing notions of germ layer homology.

This paper was not simply a doctoral student's labor in animal morphology, although that is how, under Leuckart's guidance, the work had begun. It was a canonical work of morphology, but it was also a beginning of cell lineage research, which was to become the first of those subdisciplines to be uniquely associated with Woods Hole. Close observation of the earliest processes of embryogenesis, conducted with every technical advantage to be gained from contemporary advances in microscopy, largely free of preoccupation with phylogeny and the intractable issues of origins, produced evidence of the superficiality of Haeckelian embryology *and* a new means for the analysis of emerging form in the embryo. No matter that this disposal of the phylogenetic ghost would create a substitute one: heredity borne by substances or particles of the egg. The fight about that would come later.

Whitman returned in due course to the United States, as independent a personality as he had left it; but he returned with scientific skills and habits of reasoning that incorporated most of the good, and little of the bad, of German science. He had begun early, and continued later, exorcism of the wraith that Haeckel had imposed upon embryology. But in so doing he installed what others in Woods Hole were to see as equally irrelevant for an explanation: the notion of "promorphology," or "predetermination" of the egg, in consequence of which the patterns of maturation and cleavage were irrevocably fixed. Thus fixed, the behavior of blastomeres would inevitably lead to a reinforcement of the original polarity; to the acquisition of symmetries more complex than spherical or radial, and to the programmed emergence of adult form. But the question could then rightly be asked, as it was: "Whence does the 'promorphology' arise; and why do we need it at all?"

Whitman would reply with cogency and reason, although not sufficient to convince some of the younger and newly self-confident investigators who came to

Woods Hole. But his replies were for all that cogent and in advance of their time; the former Bowdoin scholar, like the rapier-witted Thomas Reed in the Congress, gave as good as, or better than, he got. In the optimistic, civilized, relatively unpolitical atmosphere of the MBL (as in the two university departments—Clark and Chicago—that Whitman ran so autocratically), the Director could and did encourage alternative views. He could and did enlarge the scope of teaching and research, even beyond his own abilities, as changes in biology made such enlargement necessary; and he modified his own views, but without retreating from the first position that the hereditary constitution of the zygote is the primary source of information for its early development, and hence for the morphology finally achieved.

Stemming the Tide

Few were happy with the new ghost: heredity, or species-specific determinants, residing in the egg and directing its development, replacing a still vaguer sort of phylogenetic director. In Europe, the *entwicklungsmechanik* of Roux moved irresistibly toward physical and chemical interference with development as the investigative device, and hence toward the explanation of developmental events in physical and chemical terms. In America, especially at Woods Hole, there were at first murmurs and later, when T. H. Morgan joined forces with the German-American Jacques Loeb, well-spoken criticisms. They identified Whitman's hereditary determiners—and soon those implied by the work of Wilson, Conklin, Lillie, and others—as a new category of homunculi. To explain development as due to the action of "plasms" or "idiophores" in the protoplasm was for these critics no better than to explain it as the outcome of an "idea." For them, it was no explanation at all.

Whitman fought back, while at the same time encouraging the work of his opponents. He was no compulsive speaker and publisher, but his lectures and papers were strong, and his pen could, as Conklin remarked, be dipped in gall.[15] Thus, in 1894, six years after the founding of the MBL, he delivered a lecture upon "Evolution and Epigenesis," which was devoted to a scholarly attack on the gathering opposition.

> . . . The possibility—not to say probability—that *the egg is from the beginning of its existence as an individual cell definitely oriented,* has received but little attention. Many difficult questions are involved which can only be settled after the most exhaustive analysis of its structure and the most careful examination of its entire history. It is not enough to catch a fact here and there, in this or that species; the whole series of phenomena must be studied genetically, and in as many forms as possible. It often happens that we have to snatch facts as opportunity brings them within reach, regardless perhaps of their connections; but so long as they stand isolated, they are unsafe pegs to hang theories upon. Examples abound on this one question of the orientation of the egg, and the mention of 'isotropism' will recall more than one windfall of premature speculations."[16]

The windfall Whitman referred to was the growing body of evidence, derived especially from experiments on regulative eggs such as that of the sea urchin, which led the investigators to propose that the egg must be *isotropic—i.e.,* regionally homogeneous; and *therefore not predetermined.* That style of research to which Whitman referred with favor, *i.e.,* the "most exhaustive analysis of structure," was of course the style he had himself employed and to some extent pioneered in embryology. For its execution there came to the MBL a group of exceptional

scientific talents, some of them Whitman's own students, others independent. So "exhaustive" in fact were their productions that they stemmed the tide of experimentalism for a time, and—much more importantly—because the investigators were young enough to incorporate what was useful in the new experimental embryology, they became in due course experimenters themselves. At first the work was unabashed observation, but later most of them became observer-experimenters, and in the end it was one of them—E. B. Wilson—who provided the commanding synthesis of observational and experimental embryology. It was he who brought the revolution against nineteenth century natural philosophy, and the old spirits and specters, to a triumphant conclusion.[17]

Wilson, E. G. Conklin, and F. R. Lillie were the leaders of this school—at first observers and tracers of cell lineage, later experimenters, finally synthesizers. I may not in this essay examine, as it has been necessary to some extent to do for Haeckel and Whitman, the personalities and backgrounds of these men, however individual and fascinatingly different they were. To do so here would soften the focus of the argument—for it did, indeed, gather focus toward the turn of the century. Suffice it to say that these were Americans, who shared the personal styles of their American contemporaries more than they did the styles of the Europeans who came to Naples.

Thus Wilson, an accomplished cellist (whose close friendship with Anton Dohrn began with their mutual delight in a Schumann string quartet)[18] and a profound scholar, seems not to have been caught up in the politics of culture in the way the Europeans were. Much less, even, were the other two. Pragmatists, deeply committed to their work and to the immediate concerns of academic life, they and their contemporaries created in the short course of ten years a practice of embryology which was not merely American, but was in fact the vanguard of embryology.

Wilson was the first to carry out a complete cell lineage study at Woods Hole: this was his splendid work of development of the annelid, *Nereis*.[19] Conklin's descriptive work on *Crepidula* was perhaps even more elegant.[20] Though it did not excite the admiration of his doctoral supervisor, W. K. Brooks, it ranks still among the defining examples of cell lineage research. Lillie, under Whitman's direction, carried out a similar study on the lamellibranch, *Unio*.[21] Lillie records Wilson's remark to him in 1891: "I believe I am going to destroy the germ layer theory of development!"[22]

And so he, and the others, did, in the following sense: that, contrary to the convictions of two decades before, to the effect that the process of cleavage was indifferent, a mere subdivision of the egg preparatory to germ layer formation, and the germ layers thereafter strictly homologous species to species; the cleavages were in fact (at least in the forms they studied), *determined* as to plane, cell size, and timing. They showed that the germ layers arise by the early segregation of regionally different cytoplasms in consequence of the cleavages; and that the resultant germ-layers are *not* homologous in the way that was earlier believed.

A decade later, Wilson and Conklin had become experimenters as well as observers. Wilson published an impressive synthesis of the facts and arguments derived from both kinds of research in two monograph-length papers, on *Dentalium* and *Patella*.[23] Conklin's comprehensive study of "Organization and cell lineage of the ascidian egg" was published, with its many exquisitely drawn plates, by the Philadelphia Academy of Natural Sciences.[24] And by that time they had both taken full account of the issues—such as capacity for regulation after injury or blastomere displacement—raised by the experimentalists. The cell lineage chapter became the initiating chapter of all modern treatments of embryonic development.

But the later synthesis takes me ahead of my particular story. In the early 1890's, cell lineage was observation; the opposition was devoted, on the other hand, to experimental interference with the early embryo, under the rationales advanced originally by Roux and later by Hertwig, Boveri, and Driesch. They had two complaints: first, that observation alone, however painstaking, could never lead to *explanation,* since explanation should account for biological events in terms of chemistry and physics, not through the naming of unknown and unknowable "plasms." Second, that their own experiments showed, at least in the eggs *they* studied (which were, of course, rarely the same ones as the lineagists studied), that ordinary processes of early cleavage may to a very large extent be disrupted without loss of the embryo's capacity to form a normal-appearing larva. The campaign to exorcise the unknowable from a directive role in embryogenesis was in full career. Epigenesis was to be established upon a firm basis in the physical sciences, as an objective account of the egg's responses to environmental stimuli. That this thrust caused Morgan—who would later lead the emergence of a new science of genetics—to reject the idea of hereditary determiners of development, does not matter: Mendel was not yet rediscovered, nor the virtues of *Drosophila melanogaster.*

Epigenetics Uncompromising: Isotropism

Jacques Loeb was a scientific materialist, a cosmopolitan European educated amid the cultural tensions that formed the various camps of European science. Unlike many of his contemporaries in biology, he was solidly trained, not only in mechanistic physiology (including, of course, the physics and chemistry of the time), but also in philosophy. Commenting upon Loeb's background, Jeffrey Werdinger says:[25] "Like his teachers, his goal was to analyze and explain organic phenomena on the basis of physico-chemical laws and principles. Indeed, he came to regard classical nineteenth century physics as the very model of science properly understood."

Arrived at the Stazione Zoologica in the winter of 1889–90, he began a lifelong course of research on regeneration, tropisms, and animal behavior, seeking to explain them all under a simple, but comprehensive set of physical principles. At Naples he met several of the young Americans who had begun to visit regularly, and with their urging and assistance, emigrated to America, where he obtained a teaching post at Bryn Mawr College. Another young biologist was recruited to the faculty that year (1891): Thomas Hunt Morgan. Whitman, ever on the alert for new ideas backed up by solid work, was much taken with Loeb, and brought him eventually to the department at Chicago, where Whitman had gone as Chairman. Loeb came with Whitman to Woods Hole, there to found the course in General Physiology that has continued, with high distinction, to be taught ever since.

Except in these matters of origin and prior training, Loeb was not different from the other young men of his generation at the MBL. He was, perhaps, more passionate about the *broad* implications of arguments that were in progress; he had brought with him, along with the attitudes of the new physical biology, much positivist, social-progressive freight; and he applied it in his activities, his writings, and his lectures, exerting considerable influence in American scientific circles (but not, perhaps, as much as he might have done in Germany). A greater influence came, however, from the brash simplicity of his experiments, which were at the same time highly reproducible. Loeb saw no reason why explanations of development should assign *cause* to unknown, inherited factors of the cytoplasm or nucleus, or even worse, deny altogether the value of investigating cause. For him, the program

of embryology, indeed of all biology, was to discover causes—*which were certain to be ordinary, immediate, physical and chemical processes.* "Explanation" would consist in the identification of such processes.

On that basis, his criticisms of observational cell lineage research can be understood. His experimental accomplishments with embryos were regular and abundant. It is true that the first *popular* evidence of non-determinacy in cleavage (popular in the sense that it was widely discussed) was not Loeb's but that of Hans Driesch, working at Naples.[26] It is true that the capacity of some eggs to "regulate" development, *i.e.,* to compensate for loss or damage to blastomeres in early cleavage, was to some extent accepted even by the descriptive morphologists, although they contrived to believe for a while in its irrelevance. But Loeb, in America, went much further than Driesch. His was a most radical epigenesis, backed by simple experiments whose results were very difficult to explain if one believed, with Whitman, that the egg is always "predetermined, if not predelineated."

Loeb's later work on artificial parthenogenesis, and its implications for the argument here described, is too well-known to describe again. A single additional example of his work and the critique implicit in it must suffice, and it is best that it be from the early 1890's, the period of our interest. In the *Journal of Morphology,* that year, Loeb published a paper as remarkable for its brevity, and the boldness of its conclusions, as were the papers of the other side for their length and complexity. The third in a series with the general title, "Investigations in physiological morphology," this one was subtitled, simply, "Experiments on cleavage."[27]

The experiments described are a series of manipulations of the concentration and composition of salts in the sea water in which sea urchin (*Arbacia*) eggs were fertilized and allowed to develop. With careful observation, the consequences of these treatments for karyokinesis, cytokinesis, and the pattern of cleavage were recorded. Loeb made the discovery that nuclear division could take place without cleavage of the egg cytoplasm. When such undivided, multinucleate embryos were replaced in normal sea water, they cleaved, not by the normal stepwise process, but all at once into many cells (as many, Loeb thought, as there were nuclei). These experiments were very carefully controlled against the possibility of polyspermy, which was known to cause multipolar division.

Loeb argued:

> . . . the segmentation of the nucleus proceeds, although more slowly than under normal conditions, whilst no segmentation of the protoplasm is possible. The fact in itself is of some technical value, as it enables us to separate two processes which nature generally produces together. . . . In regard to our knowledge of segmentation, we see from this that the physiological conditions for segmentation of the nucleus are very different from the physiological conditions of the segmentation of the protoplasm. . . . But these experiments allow us to go one step farther and make clear one element in the complex called segmentation, namely the *physiological cause* for the segmentation of the protoplasm.

There follows a short digression on the water content of cells, the effects of different ions, and "irritability;" then by a chain of argument appropriate to the state of knowledge of the time, the conclusion: ". . . The segmentation of the protoplasm is the effect of a stimulus which the nucleus applies to the protoplasm, and which makes the protoplasm close around the nucleus."

The implication is not merely that a simple nuclear signal is the cause of cleavage, but that the *form* of the resulting blastomere is a direct result of it. It will be evident that such experiments and conclusions were very remote from the

observations and conclusions of cell lineage research. They were, in some degree, offensive to that group of investigators—although never, apparently, taken personally. It is impossible to do justice by any summary to the gadfly-quality of Loeb's results in this period. The best that can be done is to say that, save for a few cases of over-interpretation, his productions did show that there is little fixity (1) of cleavage pattern, or (2) of cell size *required* during very early development for the eventual production of a normal larva of the sea urchin; moreover, that such rules of cleavage as could be discerned implied a great capacity of the embryo for repair and "regulation," provided that the physical and chemical environment were appropriate. The emerging position, from this body of work and the work of others—Morgan and Ross Harrison in America, Theordor Boveri, Oskar Hertwig, Hans Driesch in Europe, was precisely the one that a physicist, comfortable with simplifying assumptions and absolutely committed to causal analysis, would take: that the egg (note "*the* egg," *i.e., every* egg) is isotropic; regionally homogeneous and undifferentiated; that it is through a series of physical stimuli and responses, the normal environment acting on a *tabula rasa,* that all the events of development are initiated and controlled. This was truly a Radical Epigenetics, originated by Driesch's "egg-shaking."

In the end, that original egg-shaker, faced with the inconsistencies of his own radical epigenetics alongside its truths, and with the truth of determinate cleavage in other eggs than the sea urchin, along with its uncertainties, would opt out of it and embrace a vitalism more reminiscent of Plato than of Schelling and Goethe. But Loeb did not. One can find in Loeb's lecture of 1912, delivered to the First International Congress of Monists at Hamburg, that same dedication to a purely mechanistic interpretation of life—but with better experimental justification—that is evident in his 1894 lecture at the MBL "On the limits of divisibility of living matter,"[28] which was an open challenge to the claim of an "organized," anisotropic egg cytoplasm. The difference between the two lectures is that for the Monists,[29] Loeb felt free to express his lifelong ethical convictions, and could add some of the new knowledge of mutations to them:

> Economic, social, and political conditions of ignorance and superstition may warp and inhibit the inherited instincts and thus create a civilization with a faulty or low development of ethics. Individual mutants may arise in which one or the other desirable instinct is lost, just as individual mutants without pigment may arise in animals; and the offspring of such mutants may, if numerous enough, lower the ethical status of a community. Not only is the mechanistic conception of life compatible with ethics; it seems the only conception of life which can lead to an understanding of the source of ethics.[30]

Nor did Thomas Hunt Morgan ever abandon physical mechanism and epigenetics. Indeed, his insistent rejection of predetermination, and of undefined hereditary elements directing the course of development, was surely one reason for his continued indifference to genes in development, after the rediscovery of Mendel's work; even for a time after the chromosome theory of heredity had blossomed so suddenly at Woods Hole. His entry into genetics, and his transformation of it at Columbia and in the summers at Woods Hole, had to await a simple and explicit *experimental* device by which he could analyse genes and chromosomes at the same time: the breeding of fruit-flies.

Earlier, Morgan did the same sort of embryological work as Loeb, but he brought to it stronger morphological and observational equipment (having done his doctoral research with Brooks at Johns Hopkins). In close contact with Driesch as

well as with Loeb, he complemented the work of those two with egg-shaking experiments of an unprecedented precision and thoroughness.

Morgan's progress, first as critic of predetermination and cell lineage, later as synthesizer of data from both sides, is well illustrated by experiments he conducted over a period of fifteen years at Naples and Woods Hole, employing two different egg-shaking techniques. The first was egg-shaking pure and simple, *á la* Driesch, but enhanced by a refinement of existing methods for obtaining egg fragments and isolated blastomeres from early embryos. (He shook the eggs with tiny shards of glass!) The second, following Boveri but again with innovations of technique (*e.g.*, in the use of the centrifuge), was analysis of development in embryos in which there were forced alterations of the cleavage planes. These analyses were carried out with expert cytologic technique, which made the conclusions much more detailed and less bold than they would otherwise have been. Cytologic detail then, like the best ultrastructural work today, makes the experienced observer cautious. But Morgan's conclusions stand far better, in the light of subsequent discovery, than do many of Loeb's, and better than any of Driesch's.

The following example will serve. Loeb had reported, in the summer of 1894, a series of startling experiments on "extra-ovates,"[31] masses of egg-substance extruded in the course of a brief osmotic shock caused by immersing the fertilized eggs in distilled water. (It is important to note here that, however troubled this work might have been by over-interpretation, it anticipated by many years the ligation experiments on amphibian eggs which brought Hans Spemann so much fame, and, in part, his Nobel Prize.) Loeb observed that Driesch, in shaking apart early sea urchin embryos, was able to obtain normal development from any of the first four blastomeres, but never from blastomeres of the eight cell stage or beyond. This was not, Loeb argued, the best test of the *minimum size* of a mass of "protoplasm" capable of developing into a whole larva. A better one would be somehow to divide the *uncleaved* egg into very small pieces, and to determine what kind of development those might be capable of.

The experiments were done by causing osmotic swelling of fertilized eggs in mass culture, producing small, spherical extrusions through the fertilization membrane; returning the culture to normal sea water, allowing it to develop, and then determining what minimum size of extruded (or original, *i.e.*, still within the fertilization membrane) fragment could form a pluteus. The conclusion was that a nucleated volume of material as little as one-eighth that of the whole egg could produce a pluteus larva. Moreover it did not *seem* to matter which part of the egg it was: Loeb thought that any part would do. Hence the egg is isotropic, and the limitation upon full differentiation is quantitative, *not* qualitative as the argument from cell lineage research on other species required.

There were, or should have been, quantitative questions about this work, the most obvious of which arises from the fact that Loeb had no way of deciding what fraction of all possible egg fragments behaved in this way, and could not therefore be certain that *any* part of an egg, one-eighth the original volume, would do. Nor did he provide the detailed cytological information that one would demand in order to be convinced that the eighth-volume objects were indeed "plutei," rather than asymmetric, multicellular masses. Nevertheless this work, coming after Driesch's (whose conclusions were similar), was a shock for those who thought they had reason to believe that the egg is not only polar, but regionally differentiated, with the parts of the larva laid down, before cleavage begins.

Morgan took up this line of work, but carried it out with even greater care than Loeb had done. His measurements were rigidly quantitative and they were supported

by thorough microscopical work on the fixed and stained products of the experiments. In 1895 he published the results of studies done at Naples, on "partial" larvae of the sea urchin *Sphaerechinus*.[31] Introducing them, he wrote:

> Up to the present time however some important questions in regard to these ("partial") larvae remain unanswered. For instance, we do not yet know the smallest size possible for the larvae, or whether this size varies according to the means first employed to get the fragment. We do not know whether the small larvae produce the same number of cells as do the normal, or whether they can assume the definitive form with fewer cells. The number of karyokinetic divisions that take place, and the resulting sizes of nuclei and cells are also unknown.

All these unknowns he undertook to make known, and to a large extent succeeded in doing so, although the central objection we would now apply to Loeb's work applied here as well—that there was no proof that *any* small piece whatsoever of an egg can give rise to a complete larva. That test had to wait until the brilliant microsurgical work of Hörstadius was done, forty years later; and its outcome was the both Loeb and Morgan were wrong.

Nevertheless: Morgan's very careful study confirmed the main *observations*, if not the broadest conclusions, of his predecessors, and added more to shock the predeterminists. He minced no words in the conclusion to this very complete paper:

> The conclusion is forced upon us—and I see no escape from it—that the formation of the embryo is not controlled by the form of cleavage. The plastic forces heed no cell boundaries but mould the germ-mass regardless of the way it is cut up into cells. That the forms assumed by the embryo in successive stages are not dependent on cell-division may be demonstrated in almost any egg. Whitman's conclusions receive I think strong support from the results of the experiments recorded in the preceding pages.

"Whitman's conclusions" are those offered in an earlier lecture at Woods Hole ("On the inadequacy of the cell theory"). And how Whitman must have simmered, to discover his thoughts on the matter, offered originally in a different context and in aid of quite different conclusions, here quoted in support of radical epigenesis!

It is instructive to follow Morgan's continued work on this problem, especially as described in papers published six and fifteen years later. The radicalism disappears as the breadth and incisiveness of the experiments increases. Thus the conclusion of the 1901 paper is already much softer: the reality of *determinate* cleavage is at least recognized, and the extent to which fragments of regulative eggs may develop is no longer overstated:[32]

> We see then that even in cases with a perfectly definite type of cleavage that give rise to embryos having definite relations to this cleavage there is no absolutely necessary relation between the two, for if the conditions are changed the relation may also be altered *or at least parts of the egg may invaginate that do not do so under ordinary circumstances. Nevertheless the pre-existing protoplasmic relations in the segmenting egg appear to have an important influence* on the formation of the normal embryo . . . [my emphasis].

The last paper of this group, published in 1910,[33] is a sophisticated analysis whose important conclusion, for our purpose here, is implicit in its title: "The effects of altering the position of the cleavage planes in eggs with precocious specification." The recognition is now an open one; that some degree of specification exists in *all* uncleaved eggs; in effect, a high degree—"precocious specification"—in mosaic development, and a low one in regulative. As well the development of eggs

such as that of the sea urchin might have been characterized as showing "low-but-not-zero" specification. Morgan's progress was the conversion of a radical epigenesis to epigenesis without isotropy; while the later research of Wilson and Conklin was a conversion of rigid predeterminism to a *relative* determinacy of cleavage, with recognition of the capacity for regulation and the importance of cell-cell interactions in guiding the course of embryo-formation, even in mosaic forms.

With the MBL's first decade behind it, its scope of scientific interests already greatly broadened and America still innocent of the drumbeat for war reverberating throughout Europe, these embryologists could look with satisfaction on their accomplishments, although few were yet of an age to look backward, and none rested on their laurels. In a nation that had so recently been a biological, if not wholly a scientific backwater, there were now not one or two, but a growing number of research universities, with departments whose biological faculties matched and, in some cases, surpassed their equivalents in the ancient institutions of Europe. Here was the MBL, where every summer there gathered a group of biologists who, because of the war in Europe and its attendant dislocations, surpassed in productivity and would soon surpass in influence the group that gathered at Naples. The MBL offered, moreover, advanced instruction for research students, under the guidance of that group, and hence under a teaching faculty that could nowhere be matched. This insured that the enterprise of fundamental research in biology would not merely survive in the U.S.A., but that by the law of compound interest (the mean number of trainees per trainer being greater than one) it would grow exponentially in the future.

Most important, embryology, jewel in the crown of evolution a decade earlier, had been made over into something else, something more important. Wilson had been right: cell lineage toppled the germ layer theory of development, and with it had fallen the Haeckelian paradigm of embryological research. The embryo and its doings came to center-stage in their own right, as a biological subject worthy of the most intense study because its secrets were clearly at the heart of multicellular life. Recapitulation was an irrelevancy: the stages of vertebrate embryogenesis (only) showed resemblances, and only resemblances, among genera, orders, and classes; but certainly not as between embryos of one and adults of an other. And the reasons for such resemblance had lost all value as *explanation* of development. Explanations would have to be sought within the cell and even within the molecules of the cell. The genealogical ghost had been driven out.

In the effort to rout remaining ghosts, the radical epigeneticists had attempted to find explanations for development solely in the physics and chemistry of "protoplasm," and in the stimuli and responses of the surrounding medium and the zygote, respectively. They failed, by and large, to convince. The response to them might well have been the reasonable one that, since the eggs of two different species, developing side-by-side in the same culture dish, produce two quite different embryos, and by two different patterns of cleavage and morphogenetic movement, there *must* be hereditary determinants of some kind directing development. And of course it would soon become apparent that genes on chromosomes were the likeliest although not the only candidates. For the radical epigeneticists, not yet quite reconciled, this argument retained a smell of preformationism, but it was at least a preformationism of matter, not of spirit. In some sense it was a return to the eighteenth century, and yet means by which the chemistry and physics of the postulated determinants might be investigated were already coming into being—hence Loeb's increasing concern with turning "colloid chemistry" and the "protoplasm" concept into a proper physical chemistry of proteins. That concern would

spawn, among Loeb's students and descendents, an important part of modern protein chemistry and enzymology.

Morgan, a hard-headed experimentalist and logician to the last, would continue a little too long to shave with Occam's Razor (hence, perhaps, his somewhat untidy beard); but his energy and powerful intelligence would turn him at the last—the genetics and cytogenetics of *Drosophila* having shown what it could reveal—to attempt a synthesis of genetic predetermination and epigenetic biochemistry. He did not solve the problem, but he *was* able to state it, and thereby to summarize outcomes of those exorcisms I have touched upon here, as a part of his Nobel address of 1934:[34]

> . . . it is conceivable that different batteries of genes come into action one after the other, as the embryo passes through the stages of its development. This sequence might be assumed to be an automatic property of the chain of genes. Such an assumption would, without proof, beg the whole question of embryonic development, and could not be regarded as a satisfactory solution.
>
> But it might be that in different regions of the egg there is a reaction between the kind of protoplasm present in those regions and in specific genes in the nuclei; certain being affected in one region of the egg, other genes in other regions. Such a view might give also a purely formal hypothesis to account for the differentiation of the cells in the embryo. The initial steps would be given in the regional constitution of the egg.
>
> The first responsive output of the genes would then be supposed to affect the protoplasm of the cells in which they lie. The changed protoplasm would now act reciprocally on the genes, bringing into activity additional or other batteries of genes. If true, this would give a pleasing picture of the developmental process.

Exodos

Realization of the broad possibilities offered by Morgan in that lecture was not to be until, I should judge, the early 1970's. A small volume devoted to the question of gene action and the control of embryogenesis—not the first and not necessarily the most complete of several near-contemporary volumes—was published by Max Hamburgh in 1971.[35] I recommend it, for its brevity, to the non-embryologist reader who would gain an impression of what had been done in the intervening forty years about "Theories of Differentiation." To summarize the book, which is itself a summary: a productive science of developmental genetics, imagined only dimly by Morgan, emerged, and while its main achievements were at first in identifying genes involved in later morphogenesis of various animals, it left little doubt that morphogenesis *is* under the direct control of genes. All the new insights into pathways and mechanisms of intermediary metabolism had been applied to embryos, and the energetics of development had come in a general way to be understood.

Curiously, it was through biochemistry rather than formal genetics, that the first coordinated attacks upon genetic control of *early* development, hence of determination, were mounted. Protein synthesis, now understood to be the second major step in gene action (transcription being the first), was shown to be continuous and necessary throughout development and from the very start: hence there were no "silent" periods for genetic control of development. And a large part of that synthesis was shown to be under control of genetic messengers prepared earlier—during oogenesis; thus providing an explanation for the apparent independence of some steps in pre-gastrula development from the zygotic genome, *and* an important set of candidates—now in definable chemical form—for those morphogenetic determinants upon whose existence the lineagists had staked their reputations.[36,37]

How appropriate it is that advanced embryological research should again be preoccupied, today, with cell lineage; of systems in which the differential distribution of specific and identified gene products can be traced, and in which the mechanisms by which those genes are activated or repressed differentially can be studied! I know no better general reference for the state of these issues at the time I write this—and for the embryo's ghostly intelligence, if any—than the volume of lectures given in the MBL's embryology course the summer of 1983,[38] ninety years after its first offering in a small wooden building at Woods Hole.

NOTES AND REFERENCES

[1] I am much in debt to the following for insights into the work and personalities of founders of the MBL: Garland Allen, for his *Life Science in the Twentieth Century* (Cambridge University Press, 1978), for several important papers on T. H. Morgan, and for his biography *Thomas Hunt Morgan: The Man and his Science* (Princeton University Press, 1978); Jane Maienschein, for her paper on *Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law* (*J. Hist. Biol.* **11**: 129–158, 1978) and for lectures delivered in 1984 at the MBL and at the Ischia meeting; and Jeffrey Werdinger, whose doctoral dissertation *Embryology at Woods Hole: The Emergence of a New American Biology* (1980), is available from University Microfilms, Ann Arbor, Michigan. A recent work of European history in the period of interest has been helpful: Norman Stone, *Europe Transformed: 1878–1919* (Harvard University Press, 1984). The first edition of Eric Davidson's *Gene Activity in Early Development* (Academic Press, New York, 1968) is a valuable source for cell lineage research in relation to experimental embryology.

[2] "Ghost" is no hyperbole. The common definition—the disembodied soul of a dead person—is only the second. The first, (*e.g.,* in Webster's New Collegiate Dictionary, 1981) is "The seat of life or intelligence." That one, applied to the entities imagined by natural philosophers to direct embryonic development, fits well. At worst, it is a metonymy.

[3] RUSSELL, BERTRAND. 1945. *A History of Western Philosophy,* fourteenth printing. Simon and Schuster, New York. Pp. 546 ff. The particular plain words between quotation marks were chosen for use in an editorial introduction to a series of papers on "The Mind," in *The Wilson Quarterly* **8**(5): 47 (1984).

[4] Amos Emerson Dolbear (1837–1910); physicist and inventor, Professor of Physics at Tufts College. The quoted passage is from the sixth of the MBL's *Biological Lectures* of 1895, but the reluctant conclusion that *creation* of the ether must have taken place is reached in the fifth. See *Biological Lectures.* Ginn & Company, Boston, 1896, pp. 63–82; 83–99.

[5] Sadi Carnot laid the foundation for the First Law in 1824. The grand structure was completed by William Thomson, later Lord Kelvin, 24 years later. The Second Law, which identifies the restricting principle in processes whose forms of energy include heat, was established by Clausius and Lord Kelvin in the 1850's. The next half-century saw the rise of a statistical, kinetic theory of matter, and a probabilistic definition of entropy. Toward the end of that time, a thoughtful physicist would have judged the appearance of form in a formless macroscopic object, without appropriate external work done on it, to be about as probable as the spontaneous boiling of water in a kettle held in a deep-freeze. See R. A. MILLIKAN, D. ROLLER, AND E. C. WILSON. 1937. *Mechanics, Molecular Physics, Heat & Sound.* Ginn & Co. (M.I.T. Press edition, 1965).

[6] Virtual particles in a quantum vacuum are individually undetectable, but they exist because their macroscopic consequences, such as the Casimir effect, exist. Moreover, if the "Big Bang" took place in an interval like the Planck time, 10^{-43} s, that might be considered an event of creation (were not there a "creationism" with which I reject the remotest connection). See JOHN D. BARROW AND JOSEPH SILK. 1983. *The Left Hand of Creation.* Basic Books, Inc., New York, for a modern cosmologist's view.

[7] The reference is to BARBARA W. TUCHMAN. 1966. *The Proud Tower.* Macmillan, New York.

[8] NORDENSKIÖLD, ERIK. 1928. *The History of Biology.* Translated from the Swedish by L. E. Eyre, Tudor Publishing Co., New York.

[9] Some dates: Bismarck's "blood and iron" statement was made in 1848; three wars followed in the unification of Germany under Prussian hegemony. The last, the Franco-Prussian war, ended in disaster for France. With the loss of Alsace-Lorraine, the humiliating capture of Napoleon III, and the indemnity of a billion dollars France was forced to pay, there were planted the seeds of the Great War of 1914. The German Empire under Wilhelm I was proclaimed formally on January 18, 1871, at Versailles.

[10] Although Haeckel and Gegenbaur were collaborators, and Haeckel and Anton Dohrn united for a time in friendship and in their views, Gegenbaur and Dohrn were mortal enemies. The former, especially, never lost an opportunity to malign the latter.

[11] NORDENSKIÖLD, E. *Op. cit.*, for Haeckel's antecedents; but see, for a devastating judgment of Goethe as scientist, the essay of SIR CHARLES SHERRINGTON. 1949. *Goethe on Nature and on Science*, 2nd ed. Cambridge University Press.

[12] See, *inter alia*, J. WERDINGER, *Op. cit.*, and STEPHEN JAY GOULD. 1977. *Ontogeny and Phylogeny*. Belknap Press of Harvard University, Cambridge, Massachusetts.

[13] LILLIE, F. R. 1944. *The Woods Hole Marine Biological Laboratory*, University of Chicago Press. P. 123.

[14] WHITMAN, C. O. 1878. The embryology of *Clepsine*. *Q. J. Microsc. Sci.* **18**: 215–314.

[15] LILLIE, F. R. 1944. *Op. cit.* P. 160.

[16] WHITMAN, C. O. 1895. Evolution and epigenesis. In *Biological Lectures*. Ginn & Co., Boston.

[17] WILSON, E. B. *The Cell in Development and Heredity*, Macmillan, New York, edition of 1925.

[18] GROEBEN, C. AND I. MÜLLER. 1975. Exhibition Catalogue: *The Naples Station at the Time of Anton Dohrn*. Pp. 89–90. The quartet was the A major, composed by Schumann in 1842. Elsewhere in this volume is reproduced a letter from Wilson to Dohrn (7 June 1899), signed with a cello device and quoting the cello line, starting at the 12th measure, of Beethoven's C-sharp minor string quartet, Op. 131.

[19] WILSON, E. B. 1892. The cell-lineage of *Neresis*: a contribution to the cytogeny of the annelid body. *J. Morphol.* **6**: 361–480.

[20] CONKLIN, E. G. 1897. The embryology of *Crepidula*. *J. Morphol.* **13**: 1–226.

[21] LILLIE, F. R. 1895. The embryology of Unionidae. *J. Morphol.* **10**: 1–100.

[22] LILLIE, F. R. 1944. *Op. cit.* P. 124.

[23] WILSON, E. B. 1904. Experimental studies on germinal localization. I. The germ-regions of the egg of *Dentalium*. AND *II*. Experiments on the cleavage-mosaic in *Patella* and *Dentalium*. *J. Exp. Zool.* **1**: 1–72; 197–268.

[24] CONKLIN, E. G. 1905. Organization and cell-lineage of the ascidian egg. *J. Acad. Natl. Sci. Philadelphia* **13**: 1–119.

[25] WERDINGER, J. *Op. cit.* P. 266.

[26] "Every historian is aware that the 'revolutionary moment' is rather apt to be the time in which certain previously known ideas, or theories, or doctrines receive a new turn that brings them forcibly to the minds of everyone, or are given a sudden incisiveness by new experiments . . . made in so striking a way that no one can escape considering them."

This passage is from I. Bernard Cohen, in his Introduction to Margaret G. Foley's translation of Galvani's *De Viribus Electricitatis* . . ., issued by the Burndy Library, Norwalk, Connecticut (1953).

[27] LOEB, JACQUES. 1892. Investigations in physiological morphology. III. Experiments on cleavage. *J. Morphol.* **7**: 253–263.

[28] LOEB, JACQUES. 1895. On the limits of divisibility of living matter. Pp. 55–65 in *Biological Lectures*. Ginn & Co., Boston.

[29] Monism can be traced back at least to Parmenides. It is the doctrine that all manifestations of the world are properties of a single, material unity. The Greek atomists were monists: so was Spinoza. Curiously, Haeckel was a monist. Ernst Mach (1838–1916), physicist-turned-philosopher, was the leading nineteenth century exponent. He was also a vitalist (though he would have denied it). Loeb's affinities for a doctrine that holds all phenomena, perception as well as external action, to be manifestations of an underlying material reality, can readily be understood.

[30] LOEB, JACQUES. 1912 (January). The mechanistic conception of life. Pp. 5–21 in *Pop. Sci. Monthly*.

[31] See ref. 28 for Loeb, and for Morgan: T. H. MORGAN. 1895. The 'partial' larvae of *Sphaerechinus*. *Archiv. f. Entwicklungsmech.* **2**: 81–126.

[32] MORGAN, T. H. 1901. The proportionate development of partial embryos. *Archiv. f. Entwicklungsmech.* **13**: 416–635.

[33] MORGAN, T. H. 1910. The effects of altering the position of the cleavage planes in eggs with precocious specification. *Archiv. f. Entwicklungsmech.* **29**: 205–224.

[34] This speech was published in *Scientific Monthly*, **41**: 5–18 (1935). Reproduced here is the quotation from: IAN SHINE AND SYLVIA WROBEL. 1976. *Thomas Hunt Morgan: Pioneer of Genetics*. The University Press of Kentucky, Lexington.

[35] HAMBURGH, MAX. 1971. *Theories of Differentiation*. American Elsevier Pub. Co., New York.

[36] GROSS, P. R. 1968. Biochemistry of differentiation. *Ann. Rev. Biochem.* **37**: 631–660.

[37] See also two other reviews, published fifteen years apart: P. R. GROSS. 1967. *Curr. Top. Dev. Biol.* **2**: 1–46; and E. H. DAVIDSON *et al.* 1982. *Science* **217**: 17–26.

[38] JEFFERY, W. R. AND R. A. RAFF, eds. 1983. *Time, Space, and Pattern in Embryonic Development*. MBL Lectures in Biology, Vol. 2. Alan R. Liss, Inc., New York.

Addenda to "Laying the ghost: embryonic development, in plain words," by Paul R. Gross.

PLATE I. Top: Old Main, the MBL's first teaching and research laboratory, on the site of which the Loeb Laboratory stands today. Photograph made by Baldwin Coolidge in 1893. Bottom: the first Embryology class, 1893. Coolidge photograph. C. O. Whitman at center, standing. F. R. Lillie at his far right. The four women students, left to right, are: S. Emma Keith; Elizabeth E. Bickford; Bertha M. Brown; Marie L. Minor. The blackboard inscription is "Isotropism." Others of the class are identified opposite page 91 in Lillie, 1944 (13). This and all other photographs courtesy of the Archives, MBL Library.

PLATE II. Top left: C. O. Whitman, 1908. Photograph by R. M. Strong. Top right: E. B. Wilson. Origin of photograph unknown. Bottom left: E. G. Conklin, 1922. Bottom right: F. R. Lillie, 1921. Photos of Conklin and Lillie, and of Loeb in Plate III, were taken by the legendary "Wireless Pete" of Woods Hole.

PLATE III. Left: Jacques Loeb in 1922. Right: Thomas Hunt Morgan at age 25, 1891. From the Johns Hopkins University Yearbook.

Reference: *Biol. Bull.* **168** (suppl.): 80–87. (June, 1985)

CELL INTERACTIONS: THE ROOTS OF A CENTURY OF RESEARCH

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Abstract

Only rarely have marine organisms provided experimental systems *par excellence* for concerted and continuing analyses of mechanisms of cell interactions, in either of the two main categories I consider: inductive and morphogenetic. Although there were significant findings with marine organisms from the beginning, they were frequently overshadowed, possibly because the seasonal character of research on marine organisms resulted in a focus on experiments that did not require continuity, and on comparative, rather than on mechanistic, analyses.

The roots of the study of inductive interactions—contemporary with the establishment of the Marine Biological Laboratory (MBL)—are found in the work of Chabry and Roux on the development of isolated blastomeres of an ascidian and a frog, respectively, after destruction of neighboring blastomeres. Roux's findings had a larger impact than Chabry's, in part because Roux cast his findings in larger terms than did Chabry, but also because of the differences in experimental approaches that emerged. The fact that the blastomeres of many marine embryos could be dissociated readily, lead to repeated comparative studies of the capacity for development of isolated blastomeres. The use of amphibian systems produced a drive to understand the failure of independent development; and the use of transplantation techniques resulted in the discovery of the "organizer," that set in train fifteen years of intensive and largely fruitless research on its chemical nature, punctuated by Lester Barth's demonstration of "neural differentiation without organizer."

The impact of studies of marine forms on the emergence of today's ideas on morphogenetic interactions—cell adhesion molecules, etc.—is less clear. The contributions of Herbst in dissociating embryos in calcium-free sea water, and of H. V. Wilson, and later Galtsoff, in re-aggregating sponge cells had no significant effect until after Holtfreter's far reaching studies of "tissue affinity."

Introduction

When I entered the Johns Hopkins University as a graduate student in 1946, destined to work with Professor B. H. Willier, the field of embryology, as it was then called (for the phrase "developmental biology" did not become popular until the early 1950s), was in the doldrums. There were, to be sure, a few active laboratories, with extraordinary leaders; in addition to Willier, Paul Weiss, then at Chicago, Viktor Hamburger, at Washington University, Johannes Holtfreter, at Rochester, and Victor Twitty at Stanford, come to mind. With such luminaries working in the United States, and at least an equal number in Europe—Hörstadius and Runnström; Brachet, Dalcq and Pasteels; Woerdemann and ten Cate; and Waddington and Abercrombie, why do I say the field was in the doldrums? My answer is this: each of the leading centers had its own special interests, its own special preserve. Each was tackling important problems, with the technology of the day. Still, there was *no major thrust,* no "true imperative" in the field. With the

exception of Hamburger and Willier in the United States, and Brachet and Waddington in Europe, most of the leaders in the field paid little attention to genetics. The embryology textbooks of the day commonly contained, at most, a single chapter on developmental genetics, despite the contributions of Dunn, Landauer, Wright, Hadorn, and others. (Willier *et al.*, 1955, reflects the state of the field after World War II).

The seeds of change, that would lead to a spirited renaissance of the field, had been sown in the 1930s and 1940s, by Ephrussi and Beadle, by Beadle and Tatum, by Caspersson, and by Brachet, to name only a few of the pioneers who pointed the way to the intellectual wedding of developmental biology and genetics. But they had only begun to influence the field.

Less heralded at the time were the strides taken by Holtfreter, and later by Moscona and Abercrombie, in analyzing what Holtfreter called "tissue affinity," studies that were the forerunners of today's widespread interest in "cell adhesion molecules." I shall return to these studies later under the (over simplified) heading "Cell Surface Interactions in Morphogenesis."

Let me return to the embryology of the 1940s. I observed that the field lacked a primary focus. It had not always been so. In fact, for nearly two decades, attention was focused, more in Europe than in the United States, but to a considerable degree throughout the world, on what came to be called "inductive cell interactions." Cell-cell interaction is a necessary condition for the formation of the cellular architecture of organs as well as for their organization and interconnection. The first demonstration of embryonic induction, by Spemann (1901a, 1907) and W. H. Lewis (1904, 1907a, b) provides the classic example. During normal development the optic vesicle grows out to contact the epidermis. A short time later the vesicle invaginates to form the optic cup; at the same time the epidermis at the point of contact thickens and sinks beneath the surface, following the retinal surface of the cup. Becoming detached from the epidermis, this group of cells rounds up and differentiates to form the lens, generally as a consequence of the influence of (or induction by) the optic vesicle.

The nature of induction was then, and remains today, a fascinating problem. In the 1940s however embryologists were groping—there is no better word—for a new approach, following the failure of then existing techniques to solve a problem whose solution had seemed, for a time, to be within their grasp.

Let us return to the roots of the problem.

Inductive Cell Interactions

The roots of the study of inductive interactions—contemporary with the establishment of the Marine Biological Laboratory—are found in the work of Chabry (1887; see Morgan, 1927), and Roux (1888) on the development of isolated blastomeres of an ascidian and a frog, respectively, after destruction of neighboring blastomeres. Roux's findings had a larger impact than Chabry's, in part because Roux cast his findings in larger terms than did Chabry. The questions addressed in these works are the following: Is the differentiation of a given blastomere a function of its position in the whole, *i.e.*, is it dependent upon contact or influences of neighboring cells, or is its development an act of "self-differentiation," which implies that, at a definite moment, it contains all the specific conditions for further differentiation? Isolation and defect experiments were widely used in analyzing this problem.

The blastomeres of the developing frog's egg are so closely united that their complete isolation is difficult. At the 2-cell or 4-cell stage of *Rana esculenta*, Roux

pricked one blastomere with a heated needle in order to exclude it from further development. This method is far less satisfactory than complete isolation because it is difficult to determine the extent of injury to the pricked blastomere and the effect of the punctured blastomere on the surviving blastomere. However, the following results were obtained: (1) by pricking one blastomere at the 2-cell stage, either a lateral or an anterior hemi-embryo was produced, depending on the direction of the first cleavage plane; and (2) by pricking one blastomere at the 4-cell stage, "three-quarter" embryos were produced. From these results Roux concluded that from the 4-cell stage, development is a mosaic of four essentially "self-differentiating" pieces.

In many cases the half-embryo restored the missing half. According to Roux this process, which he called "post-generation," was accomplished by utilization ("organization") of the protoplasm of the punctured blastomere by the half-embryo. It appears more likely, however, that the hot needle merely retarded development, and did not exclude the punctured blastomere from further development.

It was shortly thereafter that Driesch presented his now famous studies of the production of whole embryos from isolated blastomeres of the sea urchin. This separation was accomplished by shaking fertilized eggs in artificial sea water from which calcium had been removed, following the method of Herbst.

These contrasting observations of Roux and Driesch had far reaching consequences. Indeed, from them emerged two separate trails of research, each with its own philosophy. In his book *Experimental Embryology*, Morgan (1927) devoted five successive chapters to comparative studies of the capacity for development of isolated blastomeres, and the fate of cells and their location—the study of cell lineage. The fact that the blastomeres of many marine embryos could be dissociated readily led to an emphasis on comparative studies of the development of isolated blastomeres. As Morgan reported, "It has been found that the isolated blastomeres of sea urchins, of certain hydroids, of nemerteans, of *Amphioxus*, of fish, of *Triton* and of the frog give rise to whole embryos; while the isolated blastomeres of ctenophores, molluscs and ascidians give rise to half-embryos." In contrast, the use of amphibian systems, stemming from the observations by Roux, produced a drive to understand the failure of independent development, that is to identify that part of an embryo so crucial to the developmental process that its absence resulted in a defective embryo. It was this drive that promoted the study of cell interactions and resulted in the discovery of embryonic induction. It is this trail that I shall follow, pausing only to reflect briefly on the origins of these divergent trails of research. At this meeting, Gross has addressed the philosophic differences between the morphologists (cell lineage) and the physiologists (*Entwicklungsmechanik*). I would add only one other perception, based on E. G. Conklin's lectures and personal communications from B. H. Willier.

At the end of his career, Conklin lectured each summer in the Embryology Course at the Marine Biological Laboratory. In his lecture in the summer of 1946, he dwelt on the difficulties presented by "seasonal research" and spoke plaintively of his longing for a year-round supply of marine eggs and embryos, so that research could be undertaken on materials selected, not for their ease or convenience, but for their importance.

My own teacher, B. H. Willier, who was a student of Frank Lillie, (possibly Lillie's most successful student) spent several summers in Woods Hole, and was in fact a Trustee of the Marine Biological Laboratory. In the early 1960s, when I was considering an invitation to head the Laboratory's Embryology course, Willier advised me to accept—but with the caveat that I must not allow my summers at

the MBL to dilute my ongoing year-round research program. He went on to tell us (Clement Markert and me) that he was, in fact, repeating Frank Lillie's advice to him. According to Willier, Lillie, in his later years, often wondered aloud about the shortcomings of the MBL as a center for research (in contrast to "intellectual rejuvenation") and especially about the decisions on research direction imposed by the summer season, which tended to favor descriptive over experimental studies. Lillie was said to have observed, "Willier, that's why there are no Harrisons at the Laboratory."

Now, let me return to cell interactions. Our trail takes us largely to Europe, although as we have already observed, the contribution of Warren Lewis, a contemporary and colleague of Ross G. Harrison in Baltimore, was pivotal in the field.

We pick up the trail at Spemann's laboratory at the turn of the century, as revealed in articles he published in 1901(b), 1902, and 1903. There can be little doubt that these observations had their origin in comparative studies typical of their time. Spemann was examining the potencies of isolated blastomeres of *Triton*. When can restriction of prospective potency to prospective value be detected?

The method used in these experiments was constriction of eggs or embryos with a fine hair loop, as devised by O. Hertwig. This technique makes possible complete separation of the first two blastomeres, halves of blastulae and gastrulae. [A slight modification of the technique, in which a small cytoplasmic "bridge" is left, was used in Spemann's later, also classic studies of twinning combined with delayed nucleation (Spemann, 1914, 1918; see Weiss, 1939.).]

In one-third to one-fourth of the embryos studied the first cleavage coincides with the axis of symmetry of the gastrula. However, in the majority of embryos, the second cleavage coincides with this plane of symmetry.

Development subsequent to the application of firm constriction in the plane of the first cleavage produces two kinds of results: (1) one blastomere produces a normal embryo and the other forms a "*Bauchstück*," and (2) each of the two blastomeres produces a normal embryo. Subsequent observations revealed that in the former, the blastopore formed in and was restricted to the descendants of one blastomere only. (Spemann referred to this as the "dorsal" blastomere and to its product as the "dorsal-embryo-half.") This dorsal-embryo-half develops into a normal embryo, the ventral-embryo-half forming the *Bauchstück*.

When two embryos were formed, the lip of the blastopore was bisected by the ligature. In this case Spemann assumed that the constriction was median and complete. (With "incomplete" constriction, double-headed monsters are produced.)

Spemann concluded that the first two blastomeres are of equal potency *only* when they contain equal portions of the blastopore.

Eggs constricted in the blastula stage gave similar results leading him to conclude that even before the appearance of the blastopore, an area is present in the egg the equal division of which imparts equal potencies to both halves of the blastulae.

Thus, early in the first decade of the new century, Spemann took the first crucial step toward identifying the need for cell-cell interaction in the developing amphibian embryo.

Nor should we lose sight of the fact that Spemann himself, and Lewis in Baltimore, were, in those very years, establishing the need for "induction" in the development of the lens.

There followed a series of experiments using both isolation and recombination (transplantation) techniques in which Spemann (1918) analyzed the process of progressive determination in the urodele gastrula. The experiments carried out are,

in principle, as follows: pieces were removed from stated areas of two *Triton* gastrulae, and reciprocally transplanted; and the subsequent development of the transplant was followed. All changes were homoplastic. The results may be summarized as follows:

I. Exchange of pieces from presumptive medullary plate and presumptive epidermis:

A. *Early gastrulae:* presumptive epidermis, when transplanted to the future medullary plate area, develops into brain; presumptive medullary plate, when transplanted to the future epidermal region, becomes epidermis—development according to *position.*

B. *Late gastrulae:* presumptive epidermis, when transplanted to the future medullary plate area, develops into epidermis; presumptive medullary plate, in future epidermal region, becomes medullary plate—development according to *origin.*

C. Exchanges between one early and one yolk-plug stage gastrula: regardless of whether the "older" tissue transplanted was presumptive medullary plate or epidermis, development was *according to position.* However in every case the older tissue retains its "advantge" for several days.

II. Exchange of presumptive epidermis and the region immediately dorsal to the blastopore (early gastrulae): presumptive epidermis, transplanted to the area of the dorsal lip, produces brain; the region just dorsal to the blastopore, when transplanted to the future epidermal region, "becomes brain and notochord."

In 1918 Spemann concluded that the region above the blastopore is presumptive medullary plate; both brain and notochord develop from donor tissue; therefore the region above the blastopore is fixed in its fate (medullary plate) earlier than the rest of the medullary plate region.

This conclusion was surely incorrect, yet Spemann himself did not (in 1918) reveal serious concern about it in print. Nevertheless, he moved immediately to try to confirm and extend the 1918 study, repeating the experiments, but using heteroplastic grafts between two differently pigmented species of *Triton.* The findings, published in 1921, differed from those reported earlier, but not conclusively. Spemann again observed that the region of the blastopore became determined earlier than regions more distant from it and that there appeared to be an additional "organizing action" of the dorsal lip region when transplanted to another embryo. These suggestive findings set the stage for the definitive experiments by Spemann and Mangold (1924) which proved that a piece of the dorsal lip of the blastopore, in the process of gastrulation, exerts an organizational effect upon surrounding tissues in such a manner that it causes a secondary embryo to be formed if implanted in an indifferent place on another embryo. The grafted piece of the blastopore was therefore designated as an "organizer."

Following the discovery of the organizing power of the dorsal lip, and the demonstration by Spemann and Hilde Mangold that this capacity was not specific between closely related species, Spemann wondered how far this non-specificity might extend. At his suggestion Geinitz (1925), using both Spemann's transplantation method and O. Mangold's "Einsteck" technique, tested less closely related species.

Results of transplantation of "organizers" from *Pleurodeles waltli, Amblystoma mexicanum, Rana temporaria, R. esculenta,* and *Bombinator pachypus* to *Triton taeniatus, T. cristatus,* or *T. alpestris* hosts showed that the action of the organizer is non-specific between closely related genera, between families, and even between different orders (or sub-classes). The most successful case of the last mentioned type

is described in considerable detail. Using Spemann's method, a piece of *Bombinator* "organizer" was placed in the ventral side of a young *T. taeniatus* gastrula. It became invaginated near the host blastopore and eventually gave rise to a notochord, undifferentiated mesoderm, and somites. In addition it induced from the host tissue somites and a neural tube. Several similar but less striking cases were also mentioned. Transplants from *Bufo vulgaris* and *Hyla arborea* to *T. taeniatus* were unsuccessful. In the case of transplantation in the reverse direction (urodele to anuran) no induction occurred.

A complementary series of experiments dealt with the capacity of grafted *Bombinator* presumptive epidermis to be influenced by its position in the host. When stuck into the blastocoel it remained undifferentiated; if implanted in the surface of the *T. taeniatus* host it developed according to position, becoming epidermis or being invaginated and subsequently becoming mesoderm in the cases reported.

Geinitz observed that the more distant the phylogenetic relationship between graft and host, the less the tendency of the cells to mutually contribute to organs. He suggested that the earlier the stages used, the more successful the grafts, possibly because these may be antecedent to processes chemically differentiating the species. Most important, these experiments illustrate the lack of species-specificity of the induction process.

Geinitz's contribution was but the first in the long series of studies of the non-specificity of the induction process, further demonstrated in the series of articles by Holtfreter, of which his 1935 article is fully representative.

The discovery of the "organizer" and the revelation that it was not species specific set in train fifteen years of intensive and largely fruitless research on its chemical nature, by Spemann himself, especially in collaboration with Fischer and Wehmeier (1933), by Joseph Needham and C. H. Waddington, and their colleagues, by the leading Dutch investigators, especially Woerdeman and Raven and by E. J. Boell and collaborators. As described by Brachet (1950), at various times attention was focused on glycogens, fatty acids, sterols, and nucleoproteins. Fischer and colleagues, influenced by Holtfreter, finally concluded that no specific chemical, or group of chemicals, could be stated to be the organizer. On the other hand Needham, Waddington, and associates postulated that the active "evocator" is a sterol type substance, normally bound in a protein-glycogen-sterol complex and released normally during gastrulation, or under experimental conditions by cytolyzing agents.

It was Holtfreter, and especially Lester Barth, whose observations brought the "quest for the organizer" to a halt, just as World War II clouded the horizon. The MBL provided a platform in 1939 for Barth to first present his observations, subsequently published in 1941 as "Neural differentiation without organizer." Barth's discovery, that the course of differentiation of small aggregates of cells prepared from explants of ventral ectoderm of frog gastrulae depends upon the composition of the solution in which they are cultured lent weight to Holtfreter's ideas on the release of effectors by "mild and reversible cytolysis."

Following World War II the "quest for the organizer" continued, turning for a time to the nucleic acids, especially the ribonucleic acids as effectors (Brachet, 1950). While, in principle, cell-cell interaction involving the exchange of "information" at the point of impact by the exchange of vesicular material or by cytoplasmic bridges cannot be excluded, attention is now centered on the exchange of interactants *via* cytoplasmic bridges, specialized junctions or other mechanisms, and on signals generated at the membrane, transmitted *via* specific receptor sites and intracellular mediators like Ca^{++} and cyclic AMP to specific genes.

Indeed, the works of Barth presaged a quiet revolution that emphasized the possible importance of internal release and redistribution of inorganic ions, leading Barth and Barth to a series of contributions (1959–1974) in which they attempted to formulate a general theory of ionic regulation of normal embryonic induction.

But immediately after World War II, the revolution was quiet indeed, as students of embryology were swept up in the wave of extraordinary advances generated by the one gene-one enzyme hypothesis, leading to the emergence of nucleic acid chemistry and molecular genetics as focal fields of research.

Cell Surface Interactions in Morphogenesis

I have already remarked that the first decade of the twentieth century saw embryology come of age as an experimental science. Indeed, it was probably embryology's first "golden age," with advocates of both cell lineage and *Entwicklungsmechanik* contributing one discovery after another. The decade was capped by what Michael Abercrombie called "an astonishing stride forward in the history of biology," Ross G. Harrison's (1907, 1910) introduction of the technique of tissue culture in the study of nerve outgrowth. Less heralded at the time and less provocative in immediately opening up new vistas of experiments to be done were the observations of Harrison's contemporary, H. V. Wilson (1907, see Morgan, 1927), on the species specific aggregation of dissociated sponge cells. Neither Wilson's pioneering observations, nor the later extension of the work by Galtsoff, had a significant impact on concepts of morphogenesis for three decades. Nor did the contributions of Herbst at the turn of the century in dissociating embryos in calcium-free sea water contribute significantly in the conceptual sense. Indeed, these earlier observations came to the fore only after Holtfreter had published his classic article "Tissue affinity, a means of embryonic morphogenesis" in which he developed the concept of selective affinities between embryonic cells and tissues. He showed that when tissues of amphibian embryos are exposed to solutions of high pH they dissociate. Upon being returned to saline at a physiological pH, they reconstruct the tissue of origin. Only then did the concepts of adhesive selectivity in cell interactions, of "cell linking macromolecules" and "cell adhesion molecules" gradually emerge.

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AN EVOLUTIONARY CENTURY AT WOODS HOLE: INSTRUCTION IN INVERTEBRATE ZOOLOGY

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Abstract

Whitman, Lillie, and their successors always regarded research and instruction as complementary functions for the Marine Biological Laboratory. An invertebrate zoology course was taught each summer at Woods Hole for 90 years. It is suggested that the strengths of this course and its capacity to evolve came from the re-sorting of eight or nine instructors with diverse research interests every five years or less, within the constraints of a stable and highly structured instructional environment. A chronological summary of instructional staffs is followed by a brief survey of the invertebrate materials covered and the conceptual approaches used in instruction. The course was never a comprehensive systematic coverage of all marine invertebrates, while the teaching laboratory never provided the best conditions for teaching comparative anatomy, but was a much better place to investigate feeding mechanisms, locomotory patterns, or reproductive behavior in a reductionist fashion. Each group of eight or nine instructors, attracted by opportunities for personal research, almost inevitably included both mechanistic-physiologists and population-naturalists and the dialectic which resulted had both educational and research-generating value. The corporate body of active investigators at the MBL was sustained in part by the conditions of recruitment for both course instructors and post-course research students in invertebrate zoology.

Introduction

An invertebrate zoology course was taught each summer at Woods Hole for 90 years, for 81 of them in the same teaching laboratory on the lower floor of the south wing of Old Main. However, this was far from representing an evolutionary stasis. To a physiological ecologist turned Whig amateur recorder of its history, there was a continuing dynamic equilibrium. Doubtless professional historians given to the dialectic method (including Allen, 1979, 1981) would detect a long sustained struggle between the phyletic and the experimental students of the invertebrates, while a Namierian historian could readily compile proportionate statistics of the research publications and institutional connections of the instructors and plot the switches (sometimes acute, sometimes dampened) of interest in matters evolutionary. In this brief survey I shall try to go beyond my natural Whig celebration or encomium, and utilize a little from such alternative approaches. Two preliminary matters concern the mechanics of staffing the course and the logistics of its instructional laboratory. Both stem in part from the course's origins and antedate the establishment of it and of the Marine Biological Laboratory in 1888.

History

Staffing and laboratory logistics

"Whitman regarded research and instruction as co-ordinate functions with a single aim," noted Lillie (1944). Instruction at Penikese in 1873 and 1874, and at Annisquam in 1881–1886 (see Lillie, 1944; Maienschein, 1985) provided models for the course in marine invertebrate zoology which began with the founding of the MBL in 1888. Both Whitman and Lillie noted that instructors from a variety of home institutions could be recruited for each summer by the incentive of opportunities for research. In later years, in addition to a laboratory with healthy marine organisms and running sea water, these opportunities included an open and magnificent research library, contacts with an international group of peers, and (in some periods) access to technical equipment not available in many colleges. One result of this mode of recruiting noted in a later report on educational policy (Buck *et al.*, 1963) was that it has always been impossible to staff the invertebrate zoology course with a set of specialists in each group of marine invertebrates because it has always been more important to insist that all instructors show research distinction in experimental science.

Two other aspects of staffing are important. First, the content and conduct of the courses have always been the exclusive responsibility of the course instructors. The Director and the standing committee on instruction become directly involved only with the selection of each successive instructor-in-charge and with no other aspect of any ongoing instructional program. Secondly, we have the practice, which began early and soon became formalized for the invertebrate, embryology, and physiology courses, that the term as instructor-in-charge of an established course should not exceed five years.

Some other constraints arise from the fact noted by Lillie that the students in invertebrate zoology included undergraduates and were generally the youngest group in the summer institution. In fact, academic and calendar ages varied greatly, with one or two holders of Ph.D. or M.D. degrees in most classes. Over at least six of the decades, a majority of each class consisted of seniors and beginning graduate students (a fact which may confuse historians using our archives since many invertebrate course students would have different home institutions listed at spring acceptance and at completion of the summer course). The number of students was also larger than in the other formal courses, occasionally being over 50; in later years it was usually 35 to 45, from whom 10–12 would be selected for post-course research. In turn this dictated a larger number of instructors than in the other formal courses, usually eight, but ranging from seven to ten.

Another determinant of the evolution of invertebrate instruction at the MBL came from the architecture and furnishings of the teaching laboratory. Whitman and Lillie believed that students should give their full time during the six weeks or so of a formal summer course. Each student was thus to be assigned a private work space, which could be occupied at any time of the day or night. For 81 years, right up to the last summer (1968) before the opening of the Loeb laboratories, this was in the ground-floor laboratory of the south, or original, wing of the Old Main building and each individual space was actually a quarter of a large, wide workbench like a "Naples" table (Groeben, 1975) with two students facing two others. For most of the period, a long suite of sea-tables was placed down the middle of the laboratory between seven workbenches on each side, and these housed the students' study materials, the supply of healthy marine invertebrates.

The theme of this paper is one of structural continuity underlying functional change. By most appropriate measures, the MBL's invertebrate course made a major contribution to evolutionary biology during the last century. My thesis is that the strengths of this contribution came largely from the resorting of eight or nine instructors every five years or less (like chiasma-mandated recombination) within the constraints of a stable and highly structured instructional environment (with all the faunal diversity that can imply).

Instructors and invertebrates

It is possible to summarize, chronologically and briefly, the instructional staffing and organization of the course and then, systematically but even more briefly, the kinds of invertebrate material covered. In parts, these summaries will be obviously eclectic.

In the beginning most of the principal investigators (and founding fathers) also took part in instruction. In the years 1888 through 1895, summer students of zoology heard more than merely "highlight" lectures from E. G. Conklin, Cornelia M. Clapp, and C. O. Whitman himself. In the first year, B. H. Van Vleck who had assisted Alpheus Hyatt at Annisquam was listed as instructor. By 1896–1897, two younger instructors taking part were C. M. Child and F. R. Lillie. It may be significant that by the tenth session (1897), Whitman was referring to a Department of Investigation in Zoology and a Department of Instruction in Zoology, with the only three other individuals listed under "Officers of Instruction" forming a Department of Botany. A year later (1898), we find Zoölogy [printers or directors/editors seemed to use the diaeresis in alternate years] divided into departments of Investigation, Embryology (F. R. Lillie, Head Instructor), and Anatomy (James I. Peck, Head Instructor), with separate departments of Physiology (Jacques Loeb, Head Instructor) and of Botany (Bradley M. Davis, Head Instructor). In other printed announcements for 1898, the "Anatomy" course was described (more correctly in present usage) as a course on Morphology of Marine Invertebrates, and we can note that the students received additional lectures from Whitman, E. G. Gardiner, and V. L. Kellogg. [With the subsequent separation of the Embryology course from the Zoology group, the traditional four MBL courses—Botany, Invertebrate Zoology, Embryology, and Physiology—had been established by the beginning of the 20th century.]

In 1897, James I. Peck of Williams College, who was also acting as Assistant Director to Whitman, was instructor-in-charge of invertebrate zoology, and recorded staff discussion about course content (see below). He was succeeded in 1901 by Gilman A. Drew of the University of Maine, who subsequently became instructor-in-charge of the embryology course in 1908, and then continued as Assistant Director under Lillie for many years thereafter. Drew's last summer heading the invertebrate course was 1907, when assisting him as a regular instructor was Otto C. Glaser; the class heard lectures from Morgan, Conklin, Lillie, E. B. Wilson, and possibly Whitman. A student in the course that summer from Syracuse University was Charles Packard, and another student from Columbia University was Ethel N. Browne.

In invertebrate zoology, Drew was succeeded by Winterton C. Curtis, then of the University of Missouri (but see below), who headed the course 1907–1911. By 1916–1918, Caswell Grave, W. C. Allee, W. H. Taliaferro, and T. W. Painter were now instructors in the course, and in 1918–1919, Libbie H. Hyman was doing work on invertebrate respiration under Child's direction, but stemming directly from

Jacques Loeb's earlier investigations. Allee was in charge in 1919–1920 when a separate course on Protozoölogy under Gary N. Calkins was set up. By 1925, B. H. Willier and H. B. Baker were instructors and by 1928, B. H. Grave and Elbert C. Cole. The last fourteen instructors named include both experimentalists and naturalists. Cole was instructor-in-charge in 1932–1936, and was succeeded for 1937–1941 by T. H. Bissonette, under whom P. S. Crowell and J. S. Rankin were instructors.

Subsequent instructors-in-charge were: A. J. Waterman of Williams College (1942), John B. Buck (1943–1944), F. A. Brown Jr. (1945–1949), Lewis H. Kleinholz (1950–1954), Theodore H. Bullock (1955–1957), Grover C. Stephens (1958–1960), Clark P. Read (1961–1963), W. D. Russell-Hunter (1964–1968), James F. Case (1969–1971), Robert K. Josephson (1972–1974), and Michael J. Greenberg (1975–1977). The last ten named could all be described as comparative physiologists, and broadly the majority of their staffs could also be so described, although in fact they ranged in their own research activities from comparative biochemistry and biophysics through functional morphology to the physiological ecology of invertebrates, with only a few being additionally systematists. A few staff lists can illustrate this: for 1947 we have F. A. Brown, Jr. (in charge), W. D. Burbanck, C. G. Goodchild, John H. Lochhead, Madelene E. Pierce, W. M. Reid, Mary D. Rogick, and Talbot H. Waterman; for 1954: Lewis H. Kleinholz (in charge), John H. Lochhead, Norman A. Meinkoth, Grover C. Stephens, John M. Anderson, Muriel Sandeen, L. M. Passano, and Morris Rockstein; for 1967: W. D. Russell-Hunter (in charge), George G. Holz, Jr., Norman Millott, Eric L. Mills, James F. Case, Frank M. Fisher, Jr., Robert K. Josephson, Jonathan P. Green, Meredith L. Jones, and Hugh Y. Elder; and for 1971: James F. Case (in charge), Garth Chapman, Alan Gelperin, David C. Grant, Michael J. Greenberg, Joseph B. Jennings, Charlotte P. Mangum, James G. Morin, and Dorothy M. Skinner. In the period 1969–1977, the course was called Experimental Invertebrate Zoology, perhaps echoing a period in the thirties when the embryology course was named Experimental Embryology. In 1978, the invertebrate course was replaced by one entitled Neural Systems and Behavior under the direction of Alan Gelperin and subsequently of Ronald R. Hoy.

Potential material on invertebrates is enormous. Over the 91 years, the invertebrate zoology course attempted to increase understanding of the biology of >300,000 diverse species classified in 32 animal phyla (including two "new" phyla Pogonophora and Gnathostomulida which were added later in the 20th century, and several redefinitions during the period). For most of the nine decades, Protozoa were not included (except, for example, from 1963 to 1969), and most aspects of the biology of insects and of other land arthropods were deliberately excluded. The material was generally made more manageable by placing greater emphasis on the nine or so "major" phyla, designated as such, not merely as encompassing larger numbers of species or of individuals, but also in recent years by quantifiable ecological measures. To illustrate these, of the solar energy incorporated into green plants, a disproportionately large share flows through representatives of such major phyla as the Arthropoda and the Mollusca, whereas the energy flow through representatives of the minor phylum Entoprocta in any ecosystem is normally several orders of magnitude smaller. For the 77 years from Drew to Greenberg at least, the biology of Cnidaria, Annelida, Arthropoda, Mollusca, and Echinodermata always received considerable attention, with the extent of work on sponges, flatworms, nematodes, and invertebrate chordates varying from one instructional group to another. The other twenty-two minor phyla were usually neglected—the course was never a comprehensive systematic coverage of all kinds of marine invertebrates. Certain

naturalists among the course staffs were always dissatisfied by this (see below) as, in the early decades, were certain institutions which financially supported students for the invertebrate course.

Although this strategy was consistent for 91 years, staff debate on the tactics of appropriate neglect continued for at least 70 of them. In preparing to write this paper, I was surprised to read about a staff (and student) discussion (Peck, 1896) centering on "rapidly going over many forms, versus doing a few forms more thoroughly" reported for 4 July 1896 by James I. Peck, a discussion paralleled in 1966 by my course colleagues. We concluded, as Peck's associates apparently did, that with a heterogeneous group of students, a diversity of material should be available, but that levels of investigation were better paced individually by each student's needs. Of course, we were only echoing the training policy established even earlier for the Annisquam Laboratory by Alpheus Hyatt. Concentration upon "representative types" of invertebrates, an educational legacy of mixed value derived from Louis Agassiz, ebbed and flowed in the invertebrate course, reaching a later apogee in 1945–1949, and being as deliberately eschewed in 1961–1974.

This somewhat arbitary limitation of invertebrate groups to be studied was paralleled by some restriction of conceptual approach. Again we find considerable continuity over the 91 years in what could be a dynamic synthesis continually refashioned. The treatment of the invertebrates presented to most students was intermediate in regard to both grade of biological organization and level of concept; that is, it was concerned with whole animals considered mainly at the mechanistic-physiological and adaptive-functional levels of explanation. The structural-descriptive level was rarely emphasized, and the evolutionary-historical level only explored from time to time. It is possible that the tissue and cell grades of organization were more often added to the whole-animal and organ studies in the first three decades of the course, and that population and community interactions were considered more frequently after 1920, but whole-animal investigations remained central. Research themes recurring over the years, although with increasing sophistication of study techniques, include patterns of feeding, mechanics of locomotion, and reproductive behavior.

Value of MBL courses

The mechanistic functional morphology basic to this conceptual approach requires surprisingly little instruction in formal systematics, and little had ever been given in the Woods Hole invertebrate courses. In the last years of the Invertebrate Zoology course as such, the argument was being used that there were many other courses being taught elsewhere in the United States which dealt with the systematics and natural history of marine invertebrates at the senior undergraduate level, and therefore it was unnecessary to do this at the MBL. This argument ignored the fact that many of these courses elsewhere had been founded by "refugees" who believed, in part correctly, that these kinds of studies had always been neglected in MBL courses. I am sure that Drs. John M. Anderson, John M. Kingsbury, John S. Rankin, and Donald J. Zinn would claim that this educational mission was taken up by the newer institutions with which they were connected largely *because* it had been neglected for so long at the MBL. Clearly, this interpretation was not known to other internal critics concerned with other training programs at the MBL. I remember arguing with the late Harry Grundfest in the middle sixties that the MBL needed an invertebrate zoology course largely because American biology still needed an experimentalist counter to such natural history courses, even if only to assure an appropriate diversity of marine invertebrate systems to be used in future studies

in comparative physiology and physiological ecology. In making any comparisons between the MBL's invertebrate course and the marine invertebrate courses currently offered at the Isles of Shoals, at Duke's Beaufort Laboratory, at Avery Point, at Lewes, at Pacific Grove, and elsewhere, I would make an exception of the courses offered by the Friday Harbor Laboratories of the University of Washington, which have been closely similar to those at the MBL, and have had a similar output of investigators and publishable investigations.

Measures of the contribution of MBL courses, including invertebrate zoology, to both evolutionary and physiological biology in North America are varied. One, in some ways similar to contemporary use of citation indices by sociologists of science and by college administrators, was first used by G. A. Drew in 1923. He tabulated the number of students from the summers of 1908 to 1917 inclusive whose names had appeared in the 1922 edition of American Men of Science. By this measure 18% of all students and 12% of those from the invertebrate courses were regarded as successful investigators and college-level teachers. A larger sample (1918–1931) surveyed by Charles Packard in 1939 (Packard, 1940) yielded 29.6% of all students (49.1% of males) and 25.4% of invertebrate zoology students (47% of males). When, for federal training grant applications in 1964 and 1968, I surveyed the invertebrate classes from the early 1950's my figures were somewhat higher than Packard's. In any such survey, individual names may have consequence beyond such statistics. As a single example, significant contributions to our understanding of evolutionary processes, using distinct conceptual approaches and widely diverse invertebrate data bases, have been made by four students from this period: J. O. Corliss, M. J. West-Eberhard, J. S. Farris, and L. B. Slobodkin. Thus, ultimate as well as proximate biological causalities have been profitably explored by the invertebrate-trained cohorts. However, speculative phylogeny has never been prominent in invertebrate instruction at the MBL. At least from Drew's time onward. the instructors concerned with evolutionary (ultimate) questions or the neo-Darwinians, although usually outnumbered by those concerned with physiological (proximate) questions or the Loebians, have been population-statistical investigators with stochastic yet testable hypotheses rather than idealist morphologists.

One of the investigators at the MBL in the first years of the century does exemplify the worst aspects of the speculative schools of post-Haeckel morphology. He was William Patten who published metabiological reports on comparative anatomy in the *Journal of Morphology* and elsewhere, which postulated an origin of vertebrates in arachnids like *Limulus*. This represents a comparatively late derivative of the *Naturphilosophen* of J. W. Goethe, and is perhaps closest in concept to the publications of Lorenz Oken in the first half of the nineteenth century. Patten's reports can be contrasted with contemporary MBL work by Otto C. Glaser who was then an instructor in the zoology course. In the *Journal of Experimental Zoology* in 1907, Glaser published a paper whose title seems to anticipate the Neural Systems and Behavior course under Alan Gelperin which formally replaced the invertebrate zoology course in 1978. It was entitled "On movement and problem solving in *Ophiura*."

Instructional material from the invertebrate course continued to affect more formal pedagogy elsewhere. Many textbooks had origins at Woods Hole. Among others, Winterton C. Curtis, Chauncey G. Goodchild, Douglas A. Marsland, and Libbie H. Hyman were involved in early undergraduate texts. The only advanced invertebrate text in English remains uncompleted after Libbie H. Hyman prepared the first five magnificent volumes (1940–1954), each as a real pandect. Further, Woods Hole instructional work stimulated the first English coverage of comparative animal physiology in 1961 by C. Ladd Prosser and Frank A. Brown, Jr. Somewhat

earlier, the course instructors, along with a few associates under the editorship of Frank Brown, had produced the useful volume, *Selected Invertebrate Types* (1950). This was a worthy successor to older German *Prakticum*, as a summary of comparative invertebrate morphology for a restricted series of type invertebrates. It emerged in conversation with some of the authors, that they did not regard it as representative of what they should teach at Woods Hole, but rather as background material they would have liked all students to have known. More recently, symbiotic instructional activities in the invertebrate course are acknowledged as part of the origins for a laboratory guide to the invertebrates in 1970 by I. W. Sherman and V. G. Sherman, for two of my paperbacks (1968 and 1969), and for my larger textbook, *A Life of Invertebrates* (1979). Of course, primary research literature was continually produced. Over the last 30 years of the course, 5–9 research papers resulted each year from the summer investigations of instructors and postcourse students. In general, many distinguished investigators, many new research topics, and a wide variety of publications were produced for American science by the invertebrate zoology course at the MBL.

Constraints and Purposes

The dual mission of the MBL

For the invertebrate course, as for the MBL as a whole, the dual mission has always been to produce new biological investigators as well as new biological investigations. Successive directors (and boards of trustees) have held firm to that mission, despite recurrent pressures to cut back on instruction (or, in earlier years, to place it under the administration of one or two colleges). They have also deliberately opposed any proposals to decouple instruction from investigation at Woods Hole. In 1978, the first annual report of Paul R. Gross quotes Whitman, "Other things being equal, the investigator is always the best instructor." Charles Packard's annual report for 1940 quotes as the first point promulgated by the then committee on instruction, "The instructorships are to be regarded as aids to research." As noted in this symposium and elsewhere (Lillie, 1944; Maienschein, 1985), the prehistory of the MBL was responsible for the initial importance of instruction. This was unusual among the early marine laboratories; initially Concarneau, Naples, Plymouth, and Monaco had no great instructional committments, although provision of aquariums for the general public was important.

One other institution, the laboratory of the Scottish Marine Biological Association at Millport in Scotland, had mixed origins like the MBL (Yonge, 1972; Currie, 1983) and an early instructional mission. It was founded as a floating laboratory, the *Ark*, by John Murray (of *Challenger* fame) at Granton in 1884 and was towed to Millport (1885) on the Isle of Cumbrae in the Clyde Sea Area to join forces with Dr. David Robertson (earlier an associate and advisor of Anton Dohrn, see Groeben, 1984), and a group of Glasgow naturalists (several involved with adult education). The Association was incorporated as a non-profit company to promote research and education in marine biology, in a close parallel to the MBL. For nearly seven decades, investigation and instruction were symbiotic at Millport as at Woods Hole. However, in 1968–1970 almost all research activities were transferred from Millport to a new set of laboratory buildings at Dunstaffnage near Oban on the west coast of mainland Scotland. The Millport laboratory has been left to continue teaching and the supply of marine material for instruction elsewhere, as the University Marine Biological Station, administered jointly by London and Glasgow Universities. It is to the credit of Norman Millott and John A. Allen, successive directors of the "rump" station, that some worthy research has continued at Millport. Within fifteen

years, the Dunstaffnage laboratory has grown much more like the Woods Hole Oceanographic Institution than the MBL, and it is interesting that they are now similarly trying to re-establish tenuous links with graduate education. The dual committment to research and training at the MBL should never be compromised.

Given that the double mission has helped create the rich MBL summer environment of collective curiosity and scientific debate, what was uniquely important about the MBL's invertebrate course? My thesis suggests that both the microenvironment of the instructional setting, and the numbers, recruiting, and turnover of the instructional staff were unusual, possibly unique. Both features may merit a further gloss.

The instructional theater

The part played by the invertebrate teaching laboratory as the theater in which instruction in invertebrate zoology evolved over nearly a century, can hardly be exaggerated. The availability of healthy marine invertebrates in the tanks and dishes of the sea-tables almost mandated that over nine decades some students in every summer would pursue studies on whole animal physiology or behavior. The organization of this proscenium arch (along with the conditions of recruitment for the actors) created certain limitations as well as opportunities which remained consistent throughout the years. It is important to realize that the teaching laboratory in Old Main *never* provided the best conditions for teaching comparative anatomy, as successive instructors who had inclinations toward such classical morphology (such as Drew, or forty years later Bullock, or sixty years later Schopf) complained from time to time. It was always a much better place to study feeding mechanisms or locomotory patterns or reproductive behavior—in other words to investigate problems of whole animal physiology in a mechanistic, reductionist fashion. Thus it was entirely apt that the successor teaching laboratory, partly designed on the basis of the Old Main one, should be housed in a training building named after Jacques Loeb.

The case of Winterton C. Curtis provides a revealing excursus on student workspaces. He was a student in the Zoology Course in 1896, an independent investigator in the laboratory in the last years of the century, and later instructor and then instructor-in-charge for four years ending in 1911. He went on to head the first National Research Committee on the biological effects of radiation, and as such was responsible for obtaining early X-ray equipment both for H. J. Muller and for the MBL. As every historian knows, he was one of the expert witnesses used so effectively by Clarence S. Darrow as defense attorney in the Scopes trial in Tennessee. I first encountered Dr. Curtis, then a spry gentleman in his mid-eighties, when he came into the invertebrate teaching laboratory in Old Main to ascertain who was sitting in his old seat. He returned within an hour to present the student with some suitably inscribed books. On inquiry, I found he had been doing this for decades and, since the seating plan of Old Main did not change, the student honored each year always had a surname beginning with the letter 'B', 'C', or 'D'. He always talked for a while with the student (carefully avoiding any interference with class work). It was all very discreet and I may know more about the matter than most instructors, simply because one letter 'B', Stephen C. Brown, was subsequently a research associate of mine. Dr. Curtis continued his annual visits to Old Main until the summer of 1964; he died in 1966.

The importance of each student being assigned an individual working place, which may be occupied at any time of day or night, was established by Whitman and is confirmed as policy at several places in Lillie's account. As Curtis knew,

alphabetic assignment of places had persisted for at least six decades. What Lillie (1944) noted in his retrospect of forty years was still true in the middle sixties, and lights remained on in the invertebrate laboratory of Old Main long into most nights. Of course, the Old Main community was never totally asocial; many human interactions took place across and around the sea-tables. Temporary, and more lasting, partnerships seemed to be exogamous. Therefore, a hypothesis to be tested by a curious sociologist working our archives is that subsequent marriages involved alphabetically distant pairs.

The setting also provided an open consulting clinic on invertebrate biology for other investigators at MBL. If some physiologist's research animals became parasitized, there was always a possibility that someone (staff or student) in the teaching laboratory could identify the parasite. If a comparative biochemist wanted different sources of cartilage in invertebrates or of elastin fibers, information (and possibly living examples) could be available. A truly synergic exchange of knowledge between the collectors of the supply department and the instructors in the invertebrate laboratory extended over both the early decades and the last twenty years of the course. This occasionally took on unusually systematic aspects, with instructors providing diagnostic keys for collectors dealing with congeneric species, or collectors providing habitat details for less frequent forms. I have been told that, over a period of two intermediate decades, this commensal relationship went sour, with certain collectors being secretive not only about specific localities but also about general habitat conditions. In general, however, the workers in both the invertebrate teaching laboratory and the supply department provided cognate and complementary resources on invertebrate diversity to the rest of the Woods Hole community. A restored invertebrate zoology course could complement the functioning of the proposed Marine Resources Center in a similar way.

The prevalence of mechanistic investigations of feeding and locomotion over the years has already been noted, and was clearly stimulated by the availability of healthy animals in the sea-tables of the teaching laboratory. As early as the tenth session in 1897, a great deal of "live histology" was going on, making use of the translucency of tissues in certain invertebrates to observe microscopically subcellular processes. Productive variants of these techniques continued for eighty years, and contribute to ongoing work on the visualization of microtubules. Indirectly, the transference of such techniques used in Woods Hole to living mammalian tissues in the development of the rabbit's ear chamber by Eliot R. Clark in 1929 led, as was documented by W. E. LeGros Clark (1958), to the modernization of much vertebrate histology and to some continuing techniques of tissue culture.

Research projects in the open teaching laboratory were always carried out amidst a critical public. While on occasion an instructor or post-course student would feel somewhat over-advised, at least there was no danger that any experimental design would be deficient in controls or involve pseudoreplication. Finally, the significance of the living invertebrates in the sea-tables can be illustrated by two prohibitions which were among the very few laboratory rules for students in the course. First, histological fixatives were banned from the students' work-benches and from the sea-table area. Secondly, students were strongly discouraged from making personal collections of preserved animals or of molluscan shells. Keeping a diversity of living material available for *all* students was regarded as paramount.

Instructor turnover and dialectic

Great evolutionary strength resulted from the MBL policy that the term as instructor-in-charge of an established course should not exceed five years. This

allowed conceptual shifts as well as technological ones to occur in the invertebrate course, the one continuous feature for more than 80 years being the teaching laboratory with its healthy living marine invertebrates in the running-water sea-tables. It is clear that over part of this time, instruction in the parallel course in marine botany hardly evolved at all. A single instructor-in-charge ran that course for 18 years and, after a 3-year interval, his designated successors ran a largely unchanged course for a further 15 years. This relative stasis in instruction has created major planning difficulties in marine botany for the Director and instruction committee of the MBL to this day.

Not only the limited term for each course head, but also the larger number of instructors to be recruited, maintained the dynamic strength of the invertebrate course. All instructors *were* investigators. To put it crudely, the instructor-in-charge of any MBL course dispensed patronage in the form of opportunities for research. The single characteristic shared by all chosen as instructors has always been their predictable research yield. This is why I believe the larger size of the invertebrate course staff was important. Each group of eight or nine instructors, recruited as having research interests in different invertebrates, almost inevitably included both mechanistic-physiologists and population-naturalists, with experimentalists largely but not exclusively in the former group. Each year some aspects of a thesis-antithesis (Allen, 1979, 1981; Mayr, 1982) would be publicly renewed to the great benefit of the student group. When in the invertebrate classroom headed by Clark P. Read 24 years ago, I challenged the biochemical generalizations on invertebrate aging put forward by Bernard L. Strehler, using criticisms drawn from demographic statistics for life-cycles, I did not then realize my part in continuing an educational process of long standing. If, in similar debates, pejorative labels were used such as "tissue-grinding" *versus* "dickybird-listing," they more often referred to contrasting methodologies rather than to conceptual paradigms (as clearly perceived in other cases by our historians, see Allen, 1981; Maeinschein, 1981), and obviously sounded both more significant and more polemic to outside observers. There was often greater tolerance of the broader paradigms, and most instructors recognized (when they bothered at all) that both the evolutionary (population) and the physiological levels of explanation were of legitimate interest to biologists. In discussing students of ultimate (evolutionary) and proximate (physiological) causations, Mayr (1982) has even retrodicted the polarity back to the late sixteenth century and to the contrast between herbalist-naturalists and physician-physiologists.

Aside from their importance in an educational process, the continuously renewed debates among invertebrate course instructors generated or reconstituted a number of active research areas. A few from the last thirty years can be mentioned. Debate and research on the occurrence and nature of biological "clocks" spread from invertebrate course instructors. Revival of interest in August Pütter's theories on direct uptake of organic solutes by invertebrates had a similar history. Research controversies involving the hormones and neurohormones of arthropods moved into and out from the course. In several periods, dissension about invertebrate orientation and navigation gave rise to fruitful research. Debate on a heart-like structure in sea urchins was speculative and proved to be functionally ill-based, but gave rise to investigations of the role of the axial organ in responses to infective microorganisms in echinoderms. It is possible that a majority of such research questions would not have been debated and developed as active projects, but for the concurrence as instructors of mechanistic-physiologists and population-naturalists.

On the broader scale, invertebrate zoology and the other formal courses have provided essential recruitment (along with hierarchical selective processes) to renew the corporate body of active investigators at the MBL. Over the years, successive

directors of the MBL resisted any proposals to decouple instruction from investigation (thus avoiding the fate of the Scottish marine station at Millport), or to modify for the embryology, physiology, and invertebrate zoology courses the policy that the term of each instructor-in-charge should not exceed five years (thus avoiding the evolutionary difficulties of the marine botany course). Continuing and evolving strength of the MBL as a research community depends upon its demography being dynamic. In turn, this requires both intracohort competition (no matter how research space is assigned, accounted, or funded) and effective continuing recruitment. The latter was well served by the "research patronage" mode of recruitment for both course instructors and postcourse students.

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THE SEA URCHIN AND THE FRUIT FLY: CELL BIOLOGY AND HEREDITY, 1900–1910

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Abstract

The choice of an experimental subject particularly suitable for a specific research field opened the way for new discoveries and new theories. The sea urchin and the fruit fly, the material of choice for embryological and genetic research, symbolize two different research traditions.

Knowledge regarding these animals was vast but largely separate, with little cross fertilization, so that by the '30s little was known about the genetic system of the sea urchin, and embryological studies of *Drosophila* were just beginning.

This paper illustrates the reason for this disciplinary distinction. Embryologists concentrated on the relationships between nucleus and cytoplasm while geneticists of the "*Drosophila* Group" concentrated on the nucleus, focusing exclusively on the transmission aspects of heredity. T. H. Morgan's work forms a central focus, as he moved from an embryological concern to build a new scientific program of genetic transmission work.

Discussion

Many science historians have stressed the importance of laboratory materials for the development of research in particular fields. Such materials include: the chicken egg for von Baer's morphological theory of embryonic development, *Salamandra maculata* for Flemming's cytological investigation (because of the large size of its cells and nuclei), *Pisum sativum* for Mendel's early research on the hereditary laws (as opposed to the difficult second choice *Hieracium*), *Triton* for Spemann's experiments on the organizer, *Neurospora* for chemical genetics, and *Escherichia coli* and the T-phages for molecular biology.

The sometimes deliberate and sometimes serendipitous choice of an experimental subject suitable for a specific field has opened the way for advancement of research and theories. Much progress has depended upon the fortuitous discovery of organisms that clearly illustrate a process or a structure, or that lend themselves to convenient experimentation. For instance, Flemming's choice of organisms with long chromosomes as his research material undoubtedly helped him to elucidate the main features of mitosis. At other times the choice has been less fortunate. For example, Mendel's decision to test his theory of inheritance in *Hieracium* in order to generalize it, (as suggested by Nägeli), was certainly one of the reasons for the neglect of his work. In this genus, as we now know, parthenogenesis is common, which led Mendel to results incompatible with his original theory. De Vries's selection of *Oenothera lamarkiana* as experimental support of his own *Mutationtheorie* provides another such negative example.

The sea urchin and the fruit fly, *Paracentrotus lividus* and *Drosophila melanogaster*, the materials of choice for embryological and genetic research, positively symbolize two different research traditions. As a laboratory organism, the sea urchin

was first introduced by Hertwig in the spring of 1875, during his research on the process of fertilization. The egg in this species is small, has little yolk, and remains transparent even at high magnifications. Moreover both egg and sperm are easy to preserve. This material is therefore very suitable for embryological studies. The sea urchin was the organism on which Driesch performed his famous experiments, in 1891, separating the two first blastomeres and thereby challenging W. Roux's mosaic theory of embryonic development. In this way it became the material of choice for that part of embryology concerned with cell physiology and the mechanism of determination ("physiological morphology").

In contrast, *Drosophila* was introduced as an experimental organism for hereditary studies in W. E. Castle's laboratory around 1901. In 1906 Castle described some Mendelian characters in *Drosophila,* and T. H. Morgan started to use the fly by 1908 to induce de Vriesian mutations by exposing the larvae to radium. The following years he studied breeding in *Drosophila* in connection with evolutionary studies and found this animal a "wonderful material."[0] However, only after 1910 did he carry out the experiments which founded a new discipline, the chromosome theory of the gene.

Embryologists and geneticists studied their respective experimental objects in impressive depth, yet knowlege of these animals remained distinct, with little cross fertilization. Between 1906 and 1907 Stevens explored *Drosophila* for cytological studies, but the fruit fly did not enter the realm of "cytological animals." In the '30s, then, after three decades of Mendelism, little was known about the genetic system of the sea urchin and the embryological studies of *Drosophila* were just beginning. Why for many decades, notwithstanding the growing importance of research performed on these organisms, did these subjects of study and the questions asked of them remain so distinct?

By the 1890s experimental embryologists stressed that development was the result of factors internal to the organism itself, even though they differed on how the internal mechanisms operated. That mechanism relates to the notion of heredity, the transmission of some internal organizing factors from parents to offspring through the zygote. In particular, some embryologists thought that the entire process was determined by the organization of the egg cytoplasm prior to fertilization. They asked: what kind of factor is actually inherited? How do they control embryonic differentiation? In such a way the problems of heredity and those of embryogenesis seem to be neatly connected. Yet, the two fields, embryology and genetics, remained separated for many decades. Why? To answer such questions, it is necessary to study the historical developments of both disciplines. In particular, Morgan's shift from embryology to genetics and back to embryology, well known thanks to Garland Allen's book, provides a useful case-study for some general remarks about disciplinary relationships.[1]

Embryological work includes a variety of distinct research programs. *Entwicklungsmechanik* dominated the embryological community, at least in Europe, but this "sea urchin tradition" was in a morphological phase, even if it was a physiological morphology, looking for a causality of morphogenesis. Cell lineage was a different tradition and many of its problems were common to cytology, the morphological study of cell structure. Within the cytological tradition the main concern was the multiplication of cells and nuclei and in particular the role and behavior of chromosomes. Already in 1888 Boveri had demonstrated that the members of each pair of homologous chromosomes are qualitatively different in their hereditary determinants from members of all other pairs. Thus each chromosome pair was unique, having individuality, even when it disappeared during some phases

of cell division. Another research program, Mendelian genetics, was derived from a tradition different from chromosome studies, both theoretically and institutionally, and scientific communications between the two fields remained rare. Study of heredity was not concerned with transmission genetics but with corpuscular theories of heredity *and* embryology. The close relationship between the study of heredity and embryology prior to Mendel's rediscovery disappeared in the early XXth century.

The main point of contact between embryology and heredity was the problem of sex determination. This problem was well studied by the cell-lineage school, but it was less interesting for the typical *Entwicklungmechanicker,* who was more concerned with the very early phases of embryonic development, especially the first cell divisions. This problem lay at the boundary of the two separate disciplines: it was studied by cytologists, like E. B. Wilson, and by geneticists, like W. Bateson, L. Cuenot, and W. E. Castle, with very different methods and theories.

The various theories of sex determination current in the decade 1900–1910 fell into two general groups. One group maintained that external conditions were the primary factors in determining sex; the opposing group maintained that sex was determined only by internal factors. Cytologists generally held the first theory and geneticists the second, presenting a different form of the old dichotomy between epigenesis and preformation.

In 1902, C. E. McClung presented the first suggestion that the "accessory" chromosome, described by Henking in 1891, could be associated with sex determination in adults, on the basis of the existence of two classes of sperm, one with an accessory chromosome. Shortly afterward, in 1902, Boveri and Sutton pointed out the extraordinary similarity between the cytologically observed separation of members of each chromosome pair during gamete production and Mendel's postulated segregation of independent factors. That was evidence of the *possible* link between chromosomes and Mendelian factors. Boveri's evidence was conclusive, however, only for people already convinced of the chromosome theory, for it indicates, as Morgan wrote in 1910 "that individual chromosomes do not in any sense contain either preformed germs or determinants, or unit characters, or even stand for the production of particular organs in any sense."[2]

In 1905 Wilson's and Stevens' evidence that the accessory chromosome was the sex-determining element confirmed a close parallel between cytological observations and the determination of sex. In spite of these results, even among the supporters of the theory of chromosomal determination of sex, the conclusive evidence of these observations was weak. Wilson concluded that "great if not insuperable difficulties are encountered by any form of the assumption that these chromosomes are specifically male or female sex determinants."[3]

Richard Hertwig's work in 1906–1907, studying cross fertilization between frogs of different geographic races, furnished additional evidence that chromosomes really did have a significant role in sex determination. Those experiments showed that if one used the sperm of a single male for fertilizing different females, the normal sex ratio among the offspring would result. In contrast, fertilizing a female with sperm from different males produces quite variable results. It could be concluded that the sperm was really the sex-determining element. Morgan was highly impressed by these experiments and thereafter considered Wilson's interpretations more favorably. Nevertheless, Morgan was clearly opposed to the idea that chromosomes contain specific hereditary units. The chromosomes can have an important role in the determination of characters, but not necessarily as the carriers of genetic factors. The two roles remain quite distinct. There are two different kinds of problems: (1)

the chromosomal determination of sex and (2) sex as a Mendelian factor. One could accept the first without accepting the second. The epigenetic embryological tradition was ready to accept the causal connection between chromosomes and characters, but not the concept of the chromosomes as specific Mendelian factors. Wilson eventually concluded that "sex production stands in some relation with the chromosomes *and* can be treated from the stand point of Mendelian phenomena, as interpreted by the Sutton-Boveri chromosome theory."[4] But this was more an act of faith, the endorsement of a new theory, than the result of empirical demonstration. Wilson considered the chromosome as the Mendelian factor, "sex determination being a matter of Mendelian dominance, more specifically of chromosome dominance."

In contrast, Morgan rejected the simple version of chromosome theory as naive given the small number of chromosomes compared to the large number of inherited traits. He generalized his attack against the assumption that the nucleus must be the bearer of the hereditary qualities of the male, arguing that "the protoplasm may account for the results."[5] For Morgan, sex was determined in some way more complex than the action of a single element like the X-chromosome, in particular by the action of the cytoplasm on the hereditary material or by the relationship between nucleus and cytoplasm. In the period between 1894 and 1906 Morgan had often invoked a gradient or polarity concept of substance in the formative phenomena, in particular for regeneration. According to this theory, the fate of tissues was determined by the concentration of some particular substances in the cytoplasm.

Morgan's critiques of chromosomal determination of sex were two-fold. First the evidence was contradictory. Wilson's report that the spermatozoon having the extra chromosome produces a female every time and that the one without it produces a male was exactly the opposite of McClung's conclusion. Wilson and Stevens had studied mostly insects and concluded that males were heterozygous (XY) and females homozygous (XX) for the accessory chromosome. Punnett and Raynor had worked primarily with moths and chickens and had found just the opposite. Second, for Morgan the supposition was contradictory in itself because it suggested that the same chromosome will be female-determining in one generation and male-determining in the next.

As a consequence Morgan criticized "this modern way of referring everything to the chromosomes".[6] He decided in favor of the cytoplasmic determination of hereditary phenomena. He argued that chromosomes might fuse completely during the process of intertwining (synapsis), and thought that the union of two homologous chromosomes during synapsis was as homogeneous as when two drops of water fuse into one.[7] In other words, for Morgan the chromosomes do not contain hereditary information for individual characters of the embryo, but an embryo's hereditary traits result from the interactions of materials produced by the "entire constellation of chromosomes."[8] At this moment Morgan again heralded an epigenetic view, and stressed the importance of process as opposed to form. For him the chromosome theory and Mendelian genetics demanded "a morphological basis in the germ for the minutest phase (factor) of a definitive character." It is essentially a morphological conception with but a trace of functional concern. Mendelism "utilizes not a single finding of the science of biochemistsry . . . With an eye seeing only *particles* and a speech only symbolizing them, there is no such thing as the study of *process* possible".[9] As E. S. Russell pointed out in 1930:

> epigenesis and preformation represent two different attitudes to the problem of development, arise from two fundamentally different philosophies. The epigenetic

> view is dynamic, vitalist, physiological; the preformationist is static, deterministic, and morphological. The one stresses time or process, the other space and momentary state—the one emphasizes function, the other concentrates on form.[10]

Usually Morgan's attitude toward Mendelism prior to 1910 has been presented as a reaction against the use of metaphysical concepts such as determinants, idioplasm, biophores, micelles, etc. However, Morgan was also trying to generalize the de Vriesian theory of mutation which was based on the concept of pangenes, hereditary particles "in many respects analogous to the molecules of chemists."[12] Yet this kind of theorizing remained in the background because de Vries and Morgan were trying to deduce hereditary and evolutionary laws by indirect methods, such as breeding and selection of varieties. As an embryologist by training, Morgan was quite accustomed to the concept of material hereditary particles, the idea that the nucleus and the chromosomes in particular are directly involved in hereditary transmission. From this point of view, he was looking for a material basis of evolutionary jumps, suitable for experimental investigation. Therefore, his negative attitude towards both Mendelian genetics and the chromosomal theory can be attributed to the lack of scientific coherence between them. Only after the elucidation of the phenomenon of chiasmatype could the connection between genetical and cytological evidence be established and the idea of material factors governing heredity and embryogenesis be openly accepted.

The turning point and the beginning of the fruit fly model was Morgan's own studies on the "sex-limited" inheritance on *Drosophila melanogaster*. The appearance of the white-eyed mutant suddenly shifted Morgan's interest from evolutionary studies to heredity. The important fact was that this particular character, produced by a mutation totally different from a de Vriesean mutation, not only appeared to be a pure Mendelian character but also seemed clearly connected with sex inheritance. In explaining these results Morgan could accept the basic structure of Mendelian explanation and Wilson's and Stevens' idea that determination of sex has a chromosomal basis. Even in 1909, before the discovery of the fly with white eyes, Morgan assumed the role of a combination of hereditary factors. In order to explain the deviations from Mendelian ratios observed in 1905 with yellow mice, Cuénot had assumed the idea of selective fertilization proposed by Castle. In such a way no yellow mouse would be obtained by breeding heterozygotes since yellow factors from the sperm do not combine with yellow factors from the egg.

From his epigenetic point of view, Morgan could not accept that such trivial differences as hair color could prevent the fertilization between gametes carrying those colors. Morgan was thus skeptical about the Mendelian concept of purity of gametes and their absolute segregation during cell divisions. In consequence, he explained Cuénot's results by assuming that certain alleles always remained together rather than segregating in a random fashion. His complex mechanism assumed that yellow and gray "unit characters" stayed together in 50% of the offspring. One major point of his chromosomal theory, namely linkage, was already present as a formal concept before the discovery of the cytological phenomenon of chiasmata. But it was used against the concept of the purity of gametes. Morgan at first rejected both segregation and purity of gametes, accepting both only after his own results on sex-linked characters and cytological evidence.

If adult characters are determined by hereditary particles on chromosomes then a large number of traits must be inherited together, coupled. Coupling had already been observed by Bateson, who explained it first with the theory of attraction and repulsion and later with the theory of reduplication. The idea of "crossing-over"

based on Janssens' chiasmatype was an alternative to the complex cytological mechanism introduced by Bateson. Morgan assumed *at the same time* that "the materials that represent these factors are contained in the chromosomes" *and* that these factors that "couple" lie near each other in a linear series. These couplings can be separated by crossing over. The difference in the strength of the coupling depends on "the linear distance apart of the chromosomal materials that represents the factors." From this assumption it follows that the observed hereditary phenomena "are a simple mechanical result of the location of the materials on the chromosome, and of the method of union of homologous chromosomes." Mendelism is no longer a logical construction or a numerical system but the result of the location of the factors on the chromosomes.

Thus Morgan abandoned his agnosticism. For embryologists, the "sea urchin people," the most important question was not so much how hereditary information was transmitted from one generation to the following, but rather how that information was translated into adult characters. For an embryologist, heredity is not a problem but a prerequisite. Morgan abandoned that previous problem—how inherited information is transformed into adult characters—to study genetics or the transmission of information. He moved from the sea urchin tradition to a new *Drosophila* tradition.

Two comments are necessary. The first is that Morgan's attitude against theoretical supposition, which he often used to reject the ideas of others, was freely abandoned to accept a very powerful and innovative hypothesis. The second comment is that the bridge between cytology and genetics which Morgan stressed remained only a hope. The *Drosophila* group grasped the powerful idea of a linear disposition of factors on the chromosome introduced by Morgan and developed by Sturtevant. The group, especially the younger members who pushed Morgan in this direction, considered the chromosomes as black boxes, or perhaps as a string of black pearls.

Embryology for its part followed its own tradition without caring too much about the success and the appeal of the new research program in genetics. In the '30s Morgan returned to his first and greatest love, embryology. He felt the need for a general text on the relationships between genetics and embryology, but openly confessed to critics that he had discussed embryology *and* genetics, not their relationships.[13] Indeed no evidence was given by the *Drosophila* group about the physiological nature of genes or the way in which they interact during embryonic development. In the first decade of Mendelism, many scientists described factors in biochemical and physiological terms, like Bateson's theory of presence-absence, Castle's model of factor interaction, and G. S. Shull's explanation of the multiple characters phenomenon. However, the *Drosophila* group pushed this point into the background, as a problem too difficult to explain at the moment.

Embryology could not be interested in that kind of theory. Strong epigenetic attitudes and physiological models were directing embryology towards other concerns—that is organizer theories and chemical embryology, new forms of physiological morphology. Chemical embryology was in fact looking for a chemical explanation of morphogenetic movements, using may different substances as stimuli. Embryologists were more concerned with the larger changes in the whole organism than with the lesser qualities known to be associated with genetic action. As E. E. Just[14] said, embryologists were much more interested in the back than in the bristles on the back and more in how the eyes are built than in how they acquire their color.

In the decades of triumph of the chromosome theory, embryology was in a period of depression and the great expectations of the 1890's and the first decade of

the twentieth century were replaced by a sense of impotence towards the difficulties of understanding development.

> There was a time of discouragement. . . . The fertility of the soil seemed to have suddenly run out and tillage no longer worth while. What, more human, then, than the gold rush to genetics and general physiology?[15]

Many embryological experiments seemed to stress the role of the cytoplasm in differentiation. The destruction of the cytoplasm brought about serious disturbances of normal development, but the nucleus could be transplanted without such disturbance, at least in the earliest stages. The role of the nucleus seemed to be secondary for early cleavage and in the metabolism of the embryo, becoming important only for morphogenetic movements. Embryology, according to its own tradition, concentrated on both the nucleus and the cytoplasm; and "The prestige of success enjoyed by the gene theory might easily become a hindrance to the understanding of development by directing our attention solely to the genome, whereas cell movements, differentiation and in fact all developmental processes are actually effected by the cytoplasm."[16]

In contrast, the *Drosophila* group notwithstanding Morgan's earlier emphasis, concentrated on the nucleus, and more precisely on the chromosomes, focusing exclusively on the transmissional aspects of heredity. The cell, with its biochemistry and physiology, was considered a black box. Study of the egg produced no scientific success and therefore was considered non-scientific for the *Drosophila* group. Even if the problem of a biochemical and physiological description of the transformation of the egg into an adult is very important and, "there can be no question of the paramount importance of finding out what takes place during development," we cannot tell how much this information may lead to a better understanding of the chromosome theory. "For a knowledge of the chemistry of all the pigments in an animal or plant might still be very far removed from an understanding of the chemical constitution of the hereditary factors by whose activities these pigments are ultimately produced."[17]

The central problem of embryology in genetic terms was how embryonic cells arising from the same zygote and therefore sharing the same genetic constitutions develop along different lines during tissue differentiation. Even in 1935 this problem, the triggering mechanism of the expression of the genes, was felt to be inaccessible to scientific research. Many alternatives remained possible and Morgan in his Nobel Lecture confessed "that we must wait until experiments can be devised to help us to discriminate between these different possibilities."[18] Morgan, in order to reach a scientific theory of genetic transmission, had to abandon, for a while, his own tradition and interests to build a new tradition. Thus he abandoned the sea urchin in favor of the fruit fly.[19]

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HEREDITY UNDER AN EMBRYOLOGICAL PARADIGM: THE CASE OF GENETICS AND EMBRYOLOGY

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Introduction

In examining the history of genetics at the Marine Biological Laboratory (MBL), a curious paradox emerges: although the leader of the classical school of Mendelian heredity in the United States, Thomas Hunt Morgan (1866–1945), was a long-standing summer investigator at the MBL and brought his *Drosophila* research group to Woods Hole every summer from 1912 through 1940s, genetics as such never became incorporated into official MBL work. There were few other geneticists regularly at the Marine Biological Laboratory other than Morgan and his students; and, genetics did not get incorporated into the courses of instruction at the Laboratory (it still is not a separate course today). At the same time, embryology, so closely related conceptually and historically to the study of heredity, was from the beginning, and still remains today an official mainstay of the MBL's research and instructional program. Why should embryology have remained such a strong part of MBL work while genetics never really achieved the same status? Was this a local phenomenon peculiar to the MBL, or was it a reflection of some more general, intellectual and/or social trend within biology in the period after the rediscovery of Mendel in 1900? In attempting to answer these questions I was led to consider the larger issue of the historical relationship between genetics and embryology in the United States (and, to some extent, internationally as well) in the early decades of the twentieth century. What begins as an issue in the specific history of the Marine Biological Laboratory, broadens into the larger question of the history of twentieth century biology.

In the present paper I will explore (1) the early history of the relationship between genetics and embryology from 1890 to 1910; (2) the growing divergence between the two fields during the period to 1940, and (3) the role that T. H. Morgan himself played in creating the divergence between genetics and embryology; and finally (4) how the various factors may have been influential in causing Morgan to shift his position so profoundly. At the end of the paper, I will come back to the original paradox with regard to the MBL and suggest why, on an institutional level, the relationship between genetics and embryology seemed to mirror what was occurring on the national level.

Focussing on the role of Thomas Hunt Morgan in this historical analysis has several advantages. First, Morgan's career spanned the period during which embryology and heredity went from the holistic and unified, to the more restricted and limited view. Second, Morgan was, himself, a major architect of the split that occurred between genetics and embryology. Although he began his scientific career as an embryologist, and to some extent always remained one, he was willing to separate the study of genetics from that of embryology during a major segment of his career. Third, focusing on the work of a single individual allows a more in-depth analysis and the emergence of a more clear picture of the interrelationships of historical, social, and intellectual factors than would be possible, in the confines

of a single paper, if I included a large number of investigators, or a wider range of problems.

The Unified View of Heredity: 1890–1910

Following the lead of Charles Darwin and others, many late 19th and early 20th century biologists chose to construct synthetic theories that related the processes of genetic transmission to those of embryonic differentiation and development. Theorizers such as Ernst Haeckel (1834–1919) and August Weismann (1834–1914) saw the vertical process of "transmission" from parent to offspring and the horizontal process of "translation" of heredity potential into adult traits as part of the same fundamental process. At the same time, they made no distinction between what we would call today genotype and phenotype; rather they saw the two as inseparable, a division between potentiality and actuality as meaningless. They also saw cell nucleus and cytoplasm as an integrated whole as one constantly interacting system, each component inconceivable without the other. The theories of Haeckel and Weismann were stimulating in their synthetic power, and recognized a reality—namely that the processes of genetic transmission, embryonic development, and evolution of species were interrelated, an interrelationship all biologists, young and old, recognized.

However, as many younger biologists around the turn of the century complained, the methods of Weismann, Haeckel, and others generated theories which were nontestable, and thus could never be verified or disproven. As long as biologists indulged in this kind of theory-making, some younger investigators argued, biology would never gain a solid base as a hard science such as physics or chemistry. As I have shown elsewhere (Allen, 1978b) T. H. Morgan was among those younger biologists who sought more experimental and rigorous methods for pursuing biological problems.

While Morgan and his contemporaries rejected the speculative methods of his predecessors (including his teacher at Johns Hopkins, W. K. Brooks) they retained from them the unified view of heredity—a process embodying both genetic transmission and embryonic development. In 1910 Morgan wrote:

> We have come to look upon the problem of heredity as identical with the problem of development. The word heredity stands for those properties of the germ cells that find their expression in the developing and developed organism. When we speak of the transmission of characters from parent to offspring, we are speaking metaphorically; for we now realize that it is not characters that are transmitted to the child from the body of the parent but that the parent carries over the material, to both parent and offspring [Morgan, 1910a: p. 449].

His friend from both Hopkins and MBL days, Edwin Grant Conklin (1863–1952), held similar views. Indeed, Conklin felt strongly that the problem of heredity was *the* central issue of biology, as he stated clearly in 1908:

> Indeed, heredity is not a peculiar or unique principle for it is only similarity of growth and differentiation in successive generations. . . . In fact the whole process of development is one of growth and differentiation, and similarity of these in parents and offspring constitutes hereditary likeliness. The causes of heredity are thus reduced to the causes of successive differentiation of development, and the mechanism of heredity is merely the mechanism of differentiation [Conklin, 1908: pp. 89–90].

Conklin introduces his discussion by claiming:

> Heredity is today the central problem of biology. This problem may be approached from many sides—that of the breeder, the experimenter, the statistician, the physiologist, the embryologist, the cytologist—but the mechanism of heredity can be studied best by the investigation of the germ cells and their development [Conklin, 1908: pp. 89–90].

It is clear that for Morgan and Conklin, of all the approaches to heredity, the embryological conception was the most important and fruitful.

As part of his adherance to the unified concept of heredity, Morgan attacked the Mendelian and chromosome theories of heredity as isolating one component of the hereditary process from the other, and thus smacking of artificiality. In 1909 Morgan attacked the Mendelian theory for being preformationist, overly concerned with particles, and not with the actual process by which hereditary traits are manifested in the adult. As he wrote:

> The nature of Mendelian interpretation and description inextricably commits to the 'doctrine of particles' in the germ and elsewhere. It demands a 'morphological' basis in the germ for the minutest phase (factor) of a definitive character. It is essentially a morphological conception with but a trace of functional feature. With an eye seeing only particles and a speech only symbolizing them, there is no such thing as a study of a process possible. . . . It has been possible, I think, to show by means of what we know of the genesis of these color characters that the Mendelian description—of color inheritance at least—has strayed very wide of the facts; it has put factors in the germ cells that it is now quite certainly our privilege to remove; it is declared a discontinuity where there is now evident epigenesis [Morgan, 1909: p. 509].

In the following year he criticized the chromosome theory in much the same terms:

> It may be said in general that the particulate theory is the more picturesque or artistic conception of the developmental process. As a theory it has in the past dealt largely in symbolism and is inclined to make hard and fast distinctions. It seems to better satisfy a class of type of mind that asks for a finalistic solution, even though the solution be truly formal. But the very intellectual security that follows in the train of such theories seems to me less stimulating for further research than does the restlessness of spirit that is associated with the alternative [that is epigenetic or embryological] conception [Morgan, 1910, pp. 451–452].

What was telling to any embryologist, according to Morgan, was the propensity for those adhering to particulate theories to speak of adult traits as if they actually resided, in miniature within the fertilized egg. This was preformationism at its worst.

Just as Morgan opposed localizing the adult trait in a particle, hypothetical or real, he also opposed focusing largely on the cell nucleus as the seat of all genetic and developmental events. Those who looked to the nucleus alone, were ignoring the cytoplasm which "was the seat of the really interesting events [in embryogenesis]" (Morgan, 1897: p. 121). In these words Morgan was rejecting the recent studies by Boveri, E. B. Wilson, and many others which claimed that it was the nucleus, and specifically the chromosomes, which were the major determiners of the hereditary process.

Thus, to Morgan, as an embryologist in the early twentieth century, the problems of genetic transmission and embryonic development were inseparable. Learning about transmission of information between parents and offspring was of no value

without also learning about the development of the trait into its ultimate adult form. Quite literally, as Scott Gilbert has emphasized (1978), the Mendelian theory developed by the Morgan school began with solid roots in the field of embryology.

After 1910, however, Morgan began to reverse his position, and by 1926 had come to accept (indeed, in many respects, create) the rigorous separation of the problems of hereditary transmission from those of embryonic development. In his book, *The Theory of the Gene* (1926), Morgan's new position is clear:

> Between the characters, that furnish the data for the theory [that is, Mendelian theory] and the postulated genes, to which the characters are referred, lies the whole field of embryonic development. The theory of the gene, as here formulated, states nothing with respect to the way in which the genes are connected with the end-product, or character. The absence of information relating to this interval does not mean that the process of embryonic development is not of interest for genetics . . . but the fact remains that the sorting out of the characters in successive generations can be explained at present without reference to the way in which the gene affects the developmental process [Morgan, 1926: p. 26].

Morgan continued to believe in and even give acknowledgment to, the relationships between genetic transmission and embryonic development. But he did not know how to study this relationship in a concrete and experimental way. Hence, he settled for a distinct separation between the two. Although Morgan himself attempted to synthesize the two fields in *Embryology and Genetics* (1934), he was remarkably unsuccessful. But at least he admitted the difficulty of affecting a real synthesis. When a colleague told him of his disappointment in not seeing a synthesis between embryology and genetics in the book, Morgan is reported to have said: "Well, what did you expect? I did exactly what I said I would do in the title: I discussed embryology and I discussed genetics."

We now turn to the question of what factors affected Morgan's change from the more synthetic and holistic to the more analytical and restricted notion of heredity between 1910 and 1925.

Factors Influencing Morgan's Separation of Genetics From Embryology, 1910–1925

Several factors, both specific and general, contributed to Morgan's redefinition of the concept of heredity, and thus his separation of the study of transmission (genetics) from that of translation (embryology). Among the most prominent specific factors were the success of the Mendelian and chromosome theories in explaining his own work with *Drosophila* (after 1910), and his introduction to the genotype-phenotype conception of Wilhelm Johannsen in 1911. Among the general factors were Morgan's committment to mechanistic, materialistic (and physico-chemical) philosophy, his desire to establish a new field of biology with definite aims and boundaries, and, finally, the agricultural revolution in the United States that made funds available for genetic (as opposed to embryological) work, thus giving direction to research in transmission that went far and above that available for work in other areas of biology such as embryology. Let us see how each of these factors contributed to Morgan's change of position.

First, the specific factors. When Morgan published his first paper on the white-eyed mutant *Drosophila* (1910b), he made a clear interpretation of its inheritance pattern in Mendelian terms. He refrained, however, from associating the "factor" for eye color directly with the sex (X) chromosome. In the ensuing year, however, as more mutants were discovered and their patterns of transmission established,

Morgan quickly embraced the chromosome theory as well. The work of the Morgan group from 1911 onward, especially the study of sex-linked traits and chromosome mapping, provided the sort of material basis for the Mendelian theory that had been lacking, at least in Morgan's view, previously. Moreover, the association of Mendelian breeding results with the cytological studies of chromosome behavior and structure, had yielded what Lindley Darden and Nancy Maull termed an "interfield theory" of great predictive power (Darden and Maull, 1977). Moreover, by admitting that the material basis of heredity resides in the chromosomes, Morgan was forced to give the nucleus a greater role in the hereditary life of the cell than he had previously been willing to do. In fact, so complete was Morgan's change of view on the relative roles of nucleus and cytoplasm in governing the process of "heredity," that by 1919 he could write in a letter to his friend Jacques Loeb, that he wanted to dispel particularly the still-prevalent notion of "cytoplasmic inheritance:"

> It is this point [cytoplasmic inheritance] that I am anxious to go for, because of its widespread belief among biologists in general for which I can find absolutely no real basis except an emotional one. It is for this reason mainly that I have not hesitated to hold up as examples two of my best friends and a very famous German investigator [Morgan to Loeb, 14 May 1919; Loeb Papers, Library of Congress].

In the face of the extraordinary work on *Drosophila,* the idea of cytoplasmic influence on determination of any adult traits seemed to lose all force.

A second specific influence that seems to have been important in Morgan's development was his explicit recognition of the genotype-phenotype distinction as examined by Wilhelm Johannsen in his book of 1909, but especially in his paper for the *American Naturalist* of 1911. The content and polymical nature of Johannsen's paper, as well as its historical significance, have been well analyzed by two recent scholars, Fred Churchill (1974) and Jan Sapp (1984). Churchill was the first to point out that Johannsen made a distinction between the horizontal and vertical concepts of heredity, while Sapp was the first to emphasize that Johannsen's paper was a specific polemic against the phenotype conception, which he claimed was not amenable to rigorous experimental or mathematical analysis. To Johannsen, the phenotype was a horizontal concept, which, in terms of Ernst Haeckel's biogenetic law, was essentially an historical view. That is, the phenotype was the result of a long evolutionary process in which the ontogenetic development of the individual, interacting with its environment, produced the final appearance of the adult form. However, what was important to Johannsen was the underlying mechanism by which the phenotype was determined irrespective of environmental differences. The genotype concept was thus a vertical, and purposely ahistorical, view. To Johannsen, trained as a chemist, Mendelian genes had to be regarded as unchangeable entities, analogous to the atoms of chemistry. Just as atoms combine and recombine into various molecules, but nonetheless retain their individual properties, so too could genes combine and recombine in different genotypes in successive generations, and yet retain their own individuality. A gene for white eye remained a gene for white eye even when masked for a generation or two with a dominant gene for red eye. To Johannsen, "the fundamental nature of heredity lay hidden deep within the gamete." Only by the use of analytical and experimental methods could the nature of heredity be discovered, and the laws used for predictive purposes. Johannsen made a clear and explicit separation between the field of heredity and that of embryology. Heredity passes through the germ line only, in accordance with

Weismann's germ-plasm theory, and deals only with the genotype. Embryology, on the other hand, embodies the influence of environment as well as the whole past history of the species, and thus deals only with the phenotype. To make heredity amenable to experimental, analytical, and mathematical methods, Johannsen argued that the proper sphere of study was the genes within the gametes, and not the final expressed potential of the adult phenotype.

It is clear that Morgan must have learned about Johannsen's genotype-phenotype distinction by late 1910 or early 1911. Both men were present at the Princeton meeting of the American Society of Naturalists on 19 December 1910, where they participated in a symposium entitled "Study of Pure Lines of Genotypes." Morgan, Johannsen, and a number of other biologists addressed the genotype conception of heredity and evaluated this notion for the present study of genetics. At this conference, Johannsen gave his now-famous paper, "The Genotype Conception of Heredity," (Johannsen, 1911), and Morgan spoke on sex-limited inheritance and sexual dimorphism (Morgan, 1911). Furthermore, Johannsen was invited to spend part of the winter term of 1911 at Columbia, where it is highly unlikely that he and Morgan would not have met and discussed their mutual interests in the problems of the emerging new field of genetics. As early as 1913 Morgan makes reference to Johannsen's work in *Heredity in Sex* (Morgan, 1913) and again similar references appear in *Mechanism of Mendelian Heredity* (Morgan *et al.*, 1915). Although Morgan does not say it in so many words, I think it is safe to infer that Johannsen's phenotype-genotype distinction provided an important conceptual foundation for Morgan's growing awareness of the distinction that could be, and needed to be made, between genetics and embryology.

Among the more general factors influencing Morgan's separation of genetics and embryology was his long-standing committment to the philosophy of mechanistic materialism. Morgan had enthusiastically embraced the new mechanistic biology beginning as early as 1891 upon first meeting the German-born mechanistic philosopher Jacques Loeb when they both joined the faculty of the biology department at Bryn Mawr College that year. Later, as a result of his visits to the Stazione Zoologica in Naples, and particularly his association there with another German, Hans Driesch, Morgan's mechanistic views were renewed and strengthened with new experimental embryology. To Morgan, the mechanistic materialist philosophy meant belief in the material existence of the world, its structure in terms of separate and separable components, and the method of analysis, in which complex processes could be broken down into their simpler components and studied independently, under controlled conditions. This meant, of course, using rigorous experimental methods, and, at least in its early twentieth-century form, a committment to a kind of physico-chemical reductionism. Morgan was not as highly reductionist as Loeb, for he always had a feel for the whole organism that prevented him from embracing naive views equating the organism with a machine, or a "bag of enzymes." The key element in Morgan's mechanistic materialist philosophy, at least for understanding his willingness to go against his own earlier beliefs and separate genetics and embryology, is *analysis*. To Morgan, experiments only made sense in an analytical framework. If conditions could not be controlled, and the effects of complex systems could not be studied in isolation, then rigorous biology was not possible. It was essential to take complex processes and break them down into their component parts. The older, more inclusive concept of heredity was thus not amenable to mechanistic analysis. No satisfactory experimental techniques had been developed to isolate and study the process of embryonic differentiation—how it was controlled at the cellular, tissue, and organ-system level. However, with the

advent of the *Drosophila* work, at least one component of the broad view of heredity, namely, transmission from parent to offspring, suddenly became amenable to experimental and analytical methods. Though Morgan may have been predisposed to retain the broader definition of heredity, the newer techniques, compatible as they were with his basic philosophical orientation toward experimentation, dictated separating the broad definition into its simpler parts. The result was that Morgan focused on the transmission side of heredity for the next fifteen years.

Another general factor stimulating the rapid growth of the Mendelian chromosome theory, as opposed to embryology, was the American agricultural revolution taking place around the turn of the century. In the post-Civil War period, a number of changes had occurred in United States' economic and social organization which directly affected agricultural production. The most important was the rapid development of industry, which led to migration of workers from the farms and rural areas to the great centers of industrial production. The resulting urbanization created a great demand for food, but at the same time meant there were now fewer hands working the land. By the turn of the century, major financiers had turned their eyes toward the profitability of managed, large-scale agriculture. This meant, among other things, the development of new, faster-growing or higher-yielding crops. "Scientific agriculture" was not new at this time, but the form in which science was applied to agriculture had begun to change.

In the latter half of the nineteenth century, from Justes von Liebig onward, much research had been put into what was loosely called "agricultural chemistry." This field involved the scientific study of soils, the development of natural and chemical fertilizers, the production of animal feeds, attention to animal and plant nutrition, *etc.* While these efforts had yielded some major increases in productivity, by the late nineteenth century they had reached a limit in both extent and profitability. Fertilizers or feed additives, for instance, had to be added continually to keep up production levels. This was not so, however, with scientific breeding. The results of good breeding had a very different economic potential. In 1910 U. S. Secretary of Agriculture, James Wilson, argued openly for the study of heredity as a way of developing a more economically profitable agriculture. Writing in the opening pages of the newly founded *American Breeders Magazine,* Wilson noted that both fertilizers and animal nutritive feeds must be reapplied year after year to have the desired effects, whereas the hereditary effects obtained through scientific breeding were self perpetuating: "Heredity is a force more subtle and more marvelous than electricity. Once generated it needs no additional force to sustain it. Once new breeding values are created they continue as permanent economic forces." (Wilson, 1910: p. 5). Wilson then goes on to make his point more explicit.

> But the cost of improvements through breeding usually represents only a small fraction of the added values. The increase of products secured pays the price in a short time, and, since there is no further expense, the annual increase afterward is clear profit. The farmer will be able to retain a part of the larger production in the form of added profit and part will help to reduce the cost of living to those in the cities. Larger production on the farm will also give increased business to the transportation company, the manufacturer, and the merchant, and will provide the nation the larger product with which to hold our balance of trade. [*Ibid.*]

Wilson's enthusiasm was not mere political rhetoric. There was a widespread belief, partly catalyzed by the rediscovery of Mendel's laws in 1900, that the science of breeding was off to a new and momentous start. As Charles Rosenberg has

shown, the new genetics found an especially warm welcome in many state agricultural experiment stations, and agricultural schools (Rosenberg, 1976a, b). And, though the payoffs were not always as dramatic as Secretary Wilson and others initially imagined, the new genetics did contribute profoundly to the development of agriculture in the United States. The work of investigators such as Donald Jones (Connecticut Agricultural Station), E. M. East and later Paul Mangelsdorf (Harvard's Bussey Institution, devoted to practical and ornamental breeding), Charles Zeleny (University of Illinois), L. J. Stadler and Barbara McClintock (University of Missouri), and R. A. Emerson at Cornell (initially a state agricultural college) was all carried out in a specific agricultural context, and in many cases led directly to some practical agricultural gains (hybrid corn being one of the most notable).

That all of this was not lost on genetics, and even Morgan in particular, is evidenced by the fact that in 1918 E. B. Babcock and R. E. Clausen published one of the first and most widely used applied genetics texts, *Genetics in Relation to Agriculture,* dedicated, appropriately, to Morgan. In the Introduction to that book Babcock and Clausen state clearly the economic importance of applying known genetic principles to agricultural breeding:

> Of all the sciences that contribute to the great . . . composite which is known as agriculture none is more important economically than genetics. . . . Without doubt vast possibilities await realization through the more thorough and systematic development of our living economic resources. Such development is directly dependent on the successful utilization of genetic principles in plant and animal breeding. The science of genetics is still very young, but it is firmly established and is developing rapidly. It claims the attention of the producer of today and invites the most serious study of the agriculturists of tomorrow [Babcock and Clausen, 1918: pp. vii].

That Morgan agreed with these principles is clearly demonstrated by a memorandum that he sent to various geneticists around this same time, outlining plans for a department of genetics at Columbia University. In the opening paragraphs of that outline, Morgan stated:

> Until within recent years scientific agriculture has to do almost solely with the feeding of plants and animals. This condition arose from the fact that the persons who first became interested in developing a science of agriculture were chemists. To increase the productiveness of domesticated plants and animals by the use of fertilizers and properly proportion rations has been the goal of the great bulk of scientific work in agriculture. It is now evident, however, that this is only one side, and fundamentally the least important side, of the matter. What an animal or a plant produces is fundamentally determined by what that plant or animal *is.* The innate hereditary constitution of the individual and the race is the basis on which all improved feeding and fertilizing must end. The science of genetics (or breeding) is fundamental for all agriculture [From Morgan Folder, Raymond Pearl Papers, American Philosophical Society Library; no date on manuscript].

It must be remembered that Morgan was also one of the early members of the American Breeders Association, and attended at least two of their meetings (St. Louis, Missouri, December, 1903, and Columbia, Missouri, January, 1909) (Kimmelman, 1983: p. 194).

Funding patterns in the first decade of the twentieth century suggest that considerably more money was becoming available for agriculture-related research

than had been true in previous years. For example, the United States Department of Agriculture and the State Agricultural Experiment Station were both centers for Mendelian research after 1901. In addition, many states were developing agricultural experiment stations of their own where none had existed before (Rosenberg, 1976a, b). And, private foundations turned toward agriculture. In setting funding priorities for the newly established Carnegie Institution of Washington (1902), Andrew Carnegie was particularly interested in supporting the work of Luther Burbank. His reasons were explicitly that Burbank's much publicized new methods of grafting would have important economic results. At almost the same time the Carnegie Institution also funded Charles B. Davenport's Station for the Experimental Study of Evolution at Cold Spring Harbor, founded in 1904 with an initial grant of $34,250. By 1918 the annual budget for the Station had risen to $60,000, and by 1935 to $115,000. While all of the research carried out at the Station was not all directly agricultural, Davenport's initial goal and continued purpose always remained to study the factors influencing heredity and breeding in a variety of animals and plants. And, after 1915, Morgan's work with *Drosophila* was funded by the Carnegie Institution of Washington (starting with annual grants of $3,600 between 1915 and 1919, and jumping to an annual average of $12,000 from 1920 through 1934).

The funding for embryology, in contrast, was significantly less. The Carnegie Institution of Washington made its first grant for embryology in 1913, to F. P. Mall at the Anatomical Institute of Johns Hopkins University, for a total of $15,000. Perhaps more than anything else this comparison suggests why pursuit of the study of hereditary transmission had a certain immediacy to it which the study of embryology lacked.

I suggest, therefore, that around the turn of the century there was more than passing academic or intellectual interest in the study of heredity. Hereditary transmission had a practical, economic imperative which perhaps encouraged its isolation from other related problems such as embryonic development. It was this atmosphere that may have given some impetus, even indirectly, to the redefinition of heredity effected by Morgan and his followers after 1910. Let me emphasize clearly, however, that I am not suggesting that Morgan or other Mendelian geneticists raced toward the study of genetic transmission merely for financial gain. I am suggesting that the availability of funds *does* influence the direction for research programs when the programs can be carried out with new techniques and concepts. The important point I am trying to raise here is that the context for determining the availability of funds was not merely the academic and intellectual interest inherent in one or another field. It was more related to the social and economic imperatives present in the society at large, which encouraged funding in certain areas to a far greater extent than others.

At a more sociological level, the splitting of transmission genetics from embryonic development had an important practical consequence within the scientific community. It allowed Morgan, his immediate followers, and others who took up the Mendelian-chromosome theory, to define a new and separate field of investigation. Between 1910 and 1925 the Mendelian-chromosome theory became what Irmre Lakatos calls a full-fledged *research program* (Lakatos, 1970). Lakatos has emphasized that research programs not only consist of concepts but also of methods of research (in this case, for example, breeding coupled with cytological observations), standard protocols (for example the use of pure strains for breeding, or the correlation between breeding and cytological data), and philosophical methods, including the notion of what is proper explanation in a field (for example, mechanistic *vs.* holistic

interpretation; or the role of quantitative and mathematical thinking in scientific explanation). By establishing a research program, Lakatos points out, scientific workers define their fields and problems, thus influencing the direction of future research and the development of field-wide methods for dealing with challenges to accepted orthodoxy. For example, Morgan and his group not only rigorously defined the problems which were to become the future focus of genetic research, but also established an orthodoxy which focused almost exclusively on the cell nucleus as the center of heredity. Any attempts to discuss cytoplasmic inheritance (or what was sometimes referred to as "maternal effects") were strongly discouraged. Jan Sapp has studied the history of this subject exhaustively, and has shown how those who sought to publish on cytoplasmic inheritance, such as Tracy Sonnenborn and later his student, David Nanney, at first found their papers rejected by orthodox genetic journals (Sonneborn, 1978).

Sapp applied the idea of struggle for authority among competing fields, as developed by French sociologist Pierre Bourdieu (1975), specifically to the case of nuclear *versus* cytoplasmic genetics in the early twentieth century (Sapp, 1984). Bourdieu's idea is that scientific fields, or research programs in the Lakatosian sense, are in competition with other fields for money, students, and the opportunity to control academic or research positions. The competition is most keen among closely related fields, but exists to one degree or another between all fields. In Bourdieu's model, scientific authority, or competence, is understood as the socially recognized legitimacy of the individual to speak and act on scientific matters. The content of scientific ideas is thus seen as related to the social reality of establishing a professional niche, that is, a research program. Thus, Bourdieu sees the choice for pursuing certain theories over others, as well as the manner in which the theories are put forward, as an integral part of the social context among competing fields.

Applied to the development of genetics and its separation from embryology, Bourdieu's idea suggests the following scenario: as Mendelian genetics began to have some success dealing with the process of transmission, it became advantageous to begin determining the boundaries of the new field—that is, to establish its problems and its scope. This meant for Morgan and his group that it became increasingly advantageous to eliminate from the study of heredity itself the knotty problems of embryonic development with which Morgan himself (and others) had had little experimental success. By so doing, Morgan was able to outline what appeared to be a successful and easily approachable field of scientific endeavor. Had he insisted on working simultaneously with the problems of the development of phenotype and transmission of the genotype, it is doubtful that the field could have developed in any clear-cut way. Although he himself never renounced either his interest in embryology, or his belief that the Mendelian gene ultimately had to be interpreted in embryological terms, Morgan was pragmatic enough to see the advantage of pushing embryology aside for the time being. Developing the new field of Mendelian genetics with a strong central focus (transmission, assortment, and recombination), a set of research techniques, and most importantly some clear and immediate results, Morgan was able to attract attention, students, and (ultimately) research money in a way that would have been impossible had he insisted on studying heredity in the older, more holistic way. Morgan thus drew a boundary between the new field of genetics and the old field of embryonic development. Everything within the boundary was included in the new research program; those who would try to force upon the Mendelian-chromosome theory the burden of explaining embryonic development were told to become (or remain) "embryologists."

In putting forth this analysis I do not wish to suggest that Morgan or his group made such choices consciously, or were acting in a particularly ruthless or opportunist way to exclude certain topics from their new research program. I do want to suggest, however, that the conscious and subconscious aspects of what it means to establish a new field of research and to gain the recognition, money, and students which can result, is not a negligible factor in what constitutes the formation of a scientific research program. After all, research programs are more than merely good ideas. They involve techniques, equipment, laboratories, people, the desire for individual recognition, and money, all of which have some direct influence on the content and direction of the scientific ideas themselves.

Analysis and Conclusion

To return to the beginning of our paper, the question still remains: why did genetics not enter the mainstream of MBL courses or research? If the above analysis is correct—namely, that genetics was highly favored by funding patterns and by its adherence to mechanistic and experimental and analytical lines—it would have seemed all the more likely that it would have played a prominent role at the MBL. Here, I think, institutional factors peculiar at the MBL in the 1920s and '30s played a major part.

From its inception, the MBL had been a bastion of embryology and the attendant holistic definition of heredity inhertied from the nineteenth century. C. O. Whitman, founder and first Director of the MBL, was a morphologist and Haeckelian while pioneering the newer methods of cell lineage and experimentation. In addition, several of Morgan's contemporaries at the MBL objected to the new "genotypic" definition of heredity which Morgan was championing. In 1916 Jacques Loeb pointed out the difficult implications for embryology of the new work in heredity.

> The difficulties besetting the biologist in this problem [harmonious interaction of parts of an organism] have been rather increased than diminished by the discovery of Mendelian heredity, according to which each character is transmitted independently of any other character. Since the number of Mendelian characters in each organism is large, the posibility must be faced that the organism is merely a mosaic of independent hereditary characters. If this be the case the question arises: What moulds these independent characters into a harmonious whole? [Loeb, 1916: pp. v–vi]

A decade later F. R. Lillie, then Director of the MBL, clearly pointed out his objections to the new Mendelian conception of the gene with respect to embryological processes:

> I do not know of any sustained attempt to apply the modern theory of the gene to the problem of embryonic segregation. As the matter stands, this is one of the most serious limitations of the theory of the gene considered as a theory of the organism. We should, of course, be careful to avoid the implication that in its future development the theory of the gene may not be able to advance into this unconquered territory. But I do not see any expectation that this will be possible, even in principle, as long as the theory of the integrity of the entire gene system [*i.e.*, that all genes are present, or at least active] in all cells is maintained. If this is a necessary part of the gene theory, the phenomena of

> embryonic segregation must, I think, lie beyond the range of genetics [Lillie, 1927: p. 366].

Lillie even went on to claim that he did not foresee a future synthesis possible—at least in the late nineteenth century (by which he meant Weismannian) sense—given the new view of geneticists about what constituted heredity (Lillie, 1927: p. 367). Another critic of the Morgan school was Morgan's old friend and colleague, both from Woods Hole and Johns Hopkins days, Ross G. Harrison. Harrison wrote in 1937 that the new gene theory, as prestigious as it seemed to be, was much too one-sided. It focused only on the problem of what hereditary potentialities were passed from parent to offspring, and failed to deal in any significant way with the embryological issues (Harrison, 1973: p. 372). Beyond this, Harrison probed more deeply at the philosophical foundations of the split. He argued that geneticists were too atomistic, while embryologists sought a more holistic interpretation of the hereditary process:

> The embryologist, however, is concerned more with the larger changes in the whole organism and its primitive systems of organs than with the lesser qualities known to be associated with gene actions. As Just remarked . . . he is more interested in the back [of a fruit fly] than in the bristles on the back, and more in the eyes than the eye color [Harrison 1937: p. 372].

In addition to classical embryologists such as Lillie and Harrison, another group, namely those concerned with the problem of cytoplasmic inheritance reacted against the Morgan definition of heredity. As Jan Sapp pointed out, both Herbert Spencer Jennings and more particularly his student Tracy Sonneborn found the definition of heredity associated with the Morgan school far too limiting. In his autobiography Sonneborn described himself as a "lifelong critic of what seemed to be a blind and erroneous faith in the gene as a source of all heredity" (Sonneborn, 1978: p. 1). In the same paragraph he referred to the transmission conception of heredity as "a stifling dogma." Focusing as much attention as it did on the nucleus, and particularly the chromosomes, the Mendelian-chromosome theory, as defined by Morgan, left little room for nucleo-cytoplasmic interaction. Viktor Hamburger has pointed out that as late as 1951 the effects of this rigid separation (between genotype and phenotype and between nucleus and cytoplasm) were felt by Belgian embryologist Albert Dalcq. Arguing that classical genetics ignored the important role that cytoplasm as "an organized system" played in the process of differentiation, he wrote,

> This notion [of pattern in the cytoplasm and of the importance of the whole], so intimately tied to a pattern, is lacking in the system of concepts used by geneticists . . . [These] are based on a particularistic, atomistic viewpoint which neglects, despite everything, this other factor which resides in the totality of the organization [Dalcq (1951): p. 135; translated by Hamburger].

With this sort of a general objection widely felt among embryologists it is no wonder that the MBL was not a likely atmosphere for the development of genetics as a new field. Add to this the fact that Morgan did not like to bother himself with teaching, and was undoubtedly making no efforts to develop a genetics course on his own at MBL, the atmosphere at the Laboratory was simply not conducive to the new Mendelian genetics as an official Woods Hole research or teaching program.

In conclusion, then, what I want to emphasize is that the development of genetics as a field separate from the older, more inclusive notion of heredity, ended

up separating the study of genetics from the study of embryology. To summarize, the separation was the result of several interacting factors:

(1) A pervasive commitment among biologists—especially T. H. Morgan and his school—to mechanistic materialism and its associated analytical methods by which complex problems and/or processes are broken down into their simpler components;

(2) the conscious awareness of biologists of the useful distinction Wilhelm Johannsen had made between the genotype and the phenotype, corresponding as it did to the distinction between genetics and embryology;

(3) the rapid and exciting development of the Mendelian work with the fruit fly *Drosophila melganogaster; Drosophila* was an extremely favorable organism for the study of Mendelian and chromosome transmission;

(4) the competition between fields which makes the delineation of separate disciplines advantageous, especially to a new field trying to establish its own identity, its own areas of research focus, its own funding, and its own students;

(5) and last and perhaps most important, the agricultural context in which the study of how (and in what pattern) traits are passed on from one generation to another seeing as being greater economic—and I mean by that consciously *profit*—gain is viewed as more important than how traits develop from fertilized egg to adult. It was this agricultural imperative that translated not only into greater enthusiasm and optimism about the potential which genetics held, but also into greater financial and institutional support.

Thus, what started as a paradox about the specific institutional history of the MBL, now can be seen as part of a larger development both inside and outside the biological community. The widening gap between genetics and embryology, both conceptually and in terms of rapidity of new advances in the 1920s and '30s, was thus a result of a number of converging factors during the first several decades of the century. T. H. Morgan, an important figure at the MBL during this period, played a major role in creating that widening gap. That his own most exciting work did not find a more hospitable a home in the MBL is due to both institutional and wider intellectual/philosophical factors—to the difference in the holistic world view of the embryologists and the mechanistic, analytical world view of the geneticists. Such is the stuff of which scientific history is made.

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COMPARATIVE PHYSIOLOGY AND BIOCHEMISTRY AT THE ZOOLOGICAL STATION OF NAPLES

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The Zoological Station of Naples was planned and realized in 1872 as a research institute for zoology and morphology. Its founder and director Anton Dohrn was a zoologist and morphologist; the first assistants were zoologists Nicholaus Kleinenberg and Hugo Eisig. Zoologists and morphologists were the first guests of the new Institute: von Waldeyer-Hartz, Francis Balfour, Ray Lankester, August Weismann, Giovanni Battista Grassi, Antonio Della Valle, Oscar Schmidt, Willem Hübrecht, and others. The three publications issued by the Station, *Mittheilungen der Zoologischen Station in Neapel, Zoologischer Jahresbericht,* and *Fauna und Flora des Golfes von Neapel* dealt with zoology and botany. In 1876 Anton Dohrn added a section of Botany, and botanists also were among the first guests.

Research projects reflected the origin of the scientists themselves, but morphological studies dominated. Dohrn's original interest was morphology of the invertebrates and comparative embryology. In 1875 he published a book, *Urspriing der Wirbeltiere und das Prinzip des Functionswechsel* which was the basis for his 25 subsequent publications under the general title: *Studies on the Origin of the Vertebrate Body.* Later his main research interest centered around the problem of explaining the structure of the vertebrate head.

Although a morphologist until the end of his life, Dohrn had an unusual feeling for the significance of new scientific currents, especially the developing branches of physiology, comparative physiology, and physiological chemistry. Taking account of the rapid development of these disciplines which had sprouted in the early 1800's under the leadership of Jean Baptiste Dumas and Jean Baptiste Boussingault in France, and Johannes Müller and Justus von Liebig in Germany; fearing the competition of other countries, which already had more up-to-date marine stations; and hoping to attract and link new scientists to the Naples Institute; Dohrn built, in 1888, another building and connected it to the older one with a foot-bridge. He called the new building the Department of Physiology. Soon, however, the new facilities failed to meet the requirements of the ever-expanding field of comparative physiology, and he took the third step of his unique enterprise by adding a larger building, attached to the older one. This was finished in 1906. The Zoological Station maintained its well-known appearance until 1965, when the empty space spanned by the foot-bridge was filled with the new library. As Dohrn used to say: the three buildings give the impression of a railway or of a tramway, with an engine and two wagons. In the new Department, two sub-departments were established: one for Physiological Chemistry and the other for Animal and Comparative Physiology.

Dohrn died in 1909 and was unable to appreciate fully the tremendous impetus he had given to scientific activities of the Institute with the realization of these new sub-departments. When the history of the scientific activities of the Station is written, as I hope it will be, chronologically and with all the studies which have been carried out properly described, the scale will tip definitely towards physiology. There is, perhaps, no aspect of cell physiology or of comparative physiology and

biochemistry which has not been for a shorter or longer time the subject of important research at the Institute. It is a long line of flashing lights, some very luminous, some less so, which glows almost uninterrupted to the present time. I shall not even try to recall all of them, but I cannot avoid mentioning a few scientists who, by having worked at the Station for considerable periods, left an imprint on the scientific history of the Institute.

From 1892 to 1902, von Uexküll was head of the Physiology Department, and for ten years he carried out original and ingenious experiments on the nervous and muscular systems of marine animals. Uexküll was a pioneer of modern behavioral biology. He investigated the environmental relations, the "sphere of function" as he called it, which connect the individual to its environment.

During the same period Oscar Hertwig and Theodor Boveri laid the foundations of the mechanism of fertilization. Especially after the investigations of Boveri, the egg and the larvae of echinoderms became classic objects of cell physiology. Cytophysiological studies of the unfertilized and fertilized sea urchin egg cover a large part of the scientific history of the Station; this field has been elucidated by Monroy and by other participants of this meeting more expert than myself.

Active "customers" of the Physiology Department at the end of the last century and the beginning of this one were Silvestro Baglioni and Filippo Bottazzi, who, as human physiologists themselves, were well aware of the great importance of the expanding new disciplines of comparative physiology and physiological chemistry. From 1905 to 1909, Baglioni worked mostly on the sensory organs of cephalopods and fishes; Bottazzi carried out his well-known experiments on osmoregulation in marine animals. This line of research originated from the concept of the *milieu interieur*, formulated years before in France by Claude Bernard. The results obtained caused Bottazzi to distinguish aquatic animals as homeosmotic and pecilosmotic, a distinction which is maintained today with the modern, if not more transparent words, osmoconformers and osmoregulators. Baglioni and Bottazzi's work at the Station can be examined in their extensive chapters in the *Handbuch der Vergleichende Physiologie*, that monumental treatise edited by Winterstein between 1914 and 1925.

Martin Henze, who came to Naples in 1902, was in charge of the sub-department of Physiological Chemistry for ten years, until 1914. He made many important contributions to the chemistry of hemocyanin, the oxygen-carrying pigment which had been discovered by Léon Frédericq while working at the marine station of Roscoff. By his discovery of tyramine and other amines in the salivary glands of cephalopods, Henze was the initiator of a fruitful line of biochemical research which developed into several other biochemical and physiological fields, such as the biotoxins of marine animals and their humoral and nervous correlations. All these have been pursued at the Station until very recently by many scientists.

From 1908 to 1914, Otto Warburg spent several periods at the Station, where he carried out his first major independent work on the oxygen consumption which occurs when a sea urchin egg begins to develop after fertilization. He made the classic discovery that upon fertilization the rate of respiration rises as much as six-fold. These results, which provided the basis for his future work on the metabolism of tumor cells, are described in three of his very first papers (in Hoppe Seyler's *Zeitschrift fur Physiologische Chemie*) completed before obtaining his M.D. degree in 1911 at Heidelberg.

Warburg had exceptional skill in selecting the right kind of material for solving a specific problem. He chose the sea urchin egg (and not, for instance, the frog's egg, which was available in Heidelberg) because the amount of living matter is large

in relation to the yolk mass, and because development of the fertilized egg is very rapid, so that the changes he was looking for would take place in a short time. His aim was to demonstrate that in the course of growth chemical work must be done, and therefore the rate of energy supply must increase. This is self-evident to any student who studies biology today, but 80 years ago the experiments of earlier investigators of this problem had been inconclusive. More astonishing is that Warburg carried out his oxygen determinations not manometrically, but with the titrimetric method developed by Winkler, which he had improved and checked carefully for all possible causes of errors. The theory and practice of manometry were perfected by Warburg later, in 1920, and they were the key techniques of his later discoveries.

After 1922, the Belgian physiologists Henry Frédericq (son of Léon Frédericq) and Zeno Bacq became regular guests of the Station. Here they worked mainly on the physiology of the autonomic nervous system of cephalopods; the presence and release of noradrenaline and acetylcholine from the visceral nerves of invertebrates was the main object of their work. It was during these studies that Bacq discovered nemertine and amphiporine from marine annelids, a discovery which can be placed in another line of research, *i.e.*, biotoxins from marine animals. This original line goes back to Martin Henze, and includes among its exploiters Vittorio Erspamer, with his discovery of murexine and of eledoisin. Such research is pursued today by some members of the staff of the Station including Lucio Cariello.

In 1935, Bacq and Francesco Paolo Mazza demonstrated the presence of acetylcholine in the optical ganglia of the octopus, and identified the substance chemically. Earlier, in Germany, acetylcholine had been identified as the "*vagusstoff*" by Otto Löewi. The work of Bacq and Mazza is a keystone in the history of chemical nervous transmission, and it was the first direct demonstration of its existence in nervous tissue.

In the same line of research belongs the work of Enrico Sereni, who was in charge of the Department of Physiology for several years. Sereni was a brilliant physiologist, and among many other studies I like to remember are his ingenious experiments on nervous and humoral correlations of the activity of the chromatophores, and the peripheral nervous system in cephalopods, in collaboration with the young J. Z. Young.

Young founded another line of research, followed for many years, almost uninterrupted at the Station. His name is written in capital letters in the scientific history of the Institute. This afternoon we shall listen to a recollection by Young himself of his work on the neurophysiology of the squid and the octopus.

I close this sketch by asking once again that experts in zoology, botany, embryology, physiology, biochemistry, etc., who have worked at the Station, write the scientific history of the Institute. As a multifaceted crystal, the Zoological Station of Naples will reflect a hundred years of the history of Biology.

It has been said that we cannot conceive what the present state of biological sciences would be without the influence of the Zoological Station. This is pure rhetoric: too many rhetorical statements have been made about the Station.

I want to ask a simple and much less global question: what has been the influence of the Station on the development of Biology *in Italy*? After all, it was founded and developed in this country, and it is not irrational to suppose that exchanges occurred between this scientific institute and the rest of the Italian scientific community.

In fact, the impact of the Station on Italian zoology is enormous. As Giovanni Battista Grassi said, in the last century the Italian zoologists and botanists were more Linnaeans than Linnaeus himself. Only in later years were they influenced by the great revolution of the so-called scientific zoology, which had arisen in Germany in 1848 with the foundation of the *Zeitschrift für wissenschaftliche Zoologie*. Dohrn was a crusader of this revolution. The Italian zoologist Antonio Della Valle (to mention only one), who worked at the Station from 1878 to 1899, contributed greatly to the development of zoology in this country.

But the same did *not* occur in the physiological and biochemical sciences. This is surprising because, as I have recalled, the Station had developed more space for physiology and biochemistry than for zoology and morphological sciences. In my opinion there are several reasons for this, which deserve careful analysis, especially in consideration of the present status and of the future prospects of the Station.

Physiological and biochemical work accomplished at the Station remained almost unknown to Italian physiologists and biochemists. This was due primarily to the indolence and the rather restricted preparation of the Italian scientists. No physiologist in Italy, not even one of his pupils, was the heir of Bottazzi. Even today comparative physiology in this country is considered an eccentric discipline by traditional physiologists.

This is on one side. On the other side, the Station always refused to create something which would have even the appearance of a school of physiology. Yet the Institute had its own scientific staff; it had heads of Departments, and Assistants. And several of them, as I have recalled, succeeded in establishing productive lines of research in the Department of Physiology—in spite of the politics of the Institute, I should add.

Reinhard Dohrn used to say: "there are no positions at the Z.S., but only functions." By this rather obscure statement he meant that we were not *really* Head of the Department or Assistant, but we had to behave *as though* we were. If, in addition, we wanted to carry out scientific work, that was our business.

The *fear* that somebody on the staff might become the scientific head of a Department is the original sin at the Zoological Station. At the time of Anton Dohrn, Uexküll was fired because he wanted to be the literal leader of the Physiology Department. "Discord developed between Dohrn and Uexküll because the latter, as head of the Physiology Department, expected special treatment." This is reported in the Archives of the Station.

This is also the reason why the Station never had its *own* research programs. Of course that is not precisely true. During Anton Dohrn's lifetime the Station did carry out an ambitious program on its own. It was in fact the personal scientific program of the Director. All the Assistants (and I want to remember among them, particularly, Salvatore Lo Bianco), most of the zoologists and morphologists, foreigners as well as Italians, who crowded the Institute, even in disparate fields, centered their interests around a pillar, which was the original scientific program of the Station. But the situation changed suddenly with appearance of the Departments of Physiology and of Physiological Chemistry, since Dohrn was neither a physiologist nor a biochemist, and it was radicalized later when the Director was not even a scientist.

The Station never made a sincere effort to introduce itself to the Italian scientific community, however reluctant and narrow-minded were the Italian physiologists and biochemists. Today we are proud to recall the Nobel prizes of famous scientists who worked at the Station: Otto Löewi, Albrecht Kossel, Otto Warburg, Otto

Meyerhof, Theodor Svedberg, Albert Szent-Györgyi. How many excellent occasions those imply for shaking the sloth of the teachers, and for attracting young people from the Italian universities!

With the exception perhaps of Neapolitan students who knew the building from the outside, nobody for years, in the Italian universities, ever heard about the existence of a Zoological Station in Naples. Postgraduate students were admitted *for the first time* in 1947, when Giuseppe Reverberi obtained support via short-term grants from the Italian National Research Council. I had the good luck to be among them, and I wonder how welcome it was to have around a dozen restless, noisy young people, not used to the atmosphere of such an old and traditional Institute.

When Monroy last year told me of his plan to celebrate the hundred years of scientific activity at the Zoological Station of Naples and at the Marine Biological Laboratory in Woods Hole, I realized suddenly how different these two institutions have approached their intentions and purpose: the former aristocratic and exclusive; the other accessible and educational. We shall discuss further the biological future and the functional perspectives of the Zoological Station of Naples. I hope that the history of scientific activity at the Station, which we are sketching at this meeting, will not remain a mere academic celebration, but will rather help to define the place of this Institute in the Italian scientific community of today; what sort of relationship it can have (or must have) with the Italian universities; and with other scientific institutions. History, said the Romans, is the master of life. But history never repeats itself.

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SOME STRUGGLES OF JACQUES LOEB, ALBERT MATHEWS, AND ERNEST JUST AT THE MARINE BIOLOGICAL LABORATORY

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Abstract

Jacques Loeb led the Department of Physiology at the Marine Biological Laboratory (MBL) in 1892, four years after the opening of the Laboratory. In that year he was also the first to study the development of fertilized sea urchin (*Arbacia punctulata*) eggs and detected a selective effect of hypertonic sea water in eliciting nuclear cleavage. By 1899 he had discovered artificial parthenogenesis. His priority in this discovery was challenged by an assistant in his Department, A. P. Mathews, who criticized other aspects of Loeb's work both from the MBL and from their common University. Mathews also leaked Loeb's progress to the press. Loeb attempted to have Mathews fired, but Mathews remained as head of the course at the MBL and also became Professor at the University of Chicago after Loeb left. Loeb worked for over a decade to prove Mathews incorrect in his claims and criticism. Loeb's work eventually helped to destroy a colloidal theory which Mathews upheld in his book, the first American text of biochemistry. For over two decades, Mathews taught, advised, and encouraged E. E. Just, who in support of the embryological work of another mentor, F. R. Lillie, publicly attacked Loeb's work. Loeb's antipathy to Just has been attributed to racism, but possibly resulted in large part from his scientific differences with Mathews, Lillie, and Just.

Introduction

For at least the past thirty years, there has been a poker game in Woods Hole each Thursday night of every summer. Although the participants have all been eminent practitioners of a reductionist quantitative biology at the MBL, the "poker games" have consisted of a variety of different card games in which winning has depended on large components of luck coupled with concentrated study by the players. Almost uniformly the games have included "wild cards" or "jokers", *i.e.*, either the cards can be whatever the players would like or the rules have been altered to permit hidden surprises. In maximizing chance the participants have relaxed by deliberately changing their habits of work, and have appealed to the power of the unknown.

Reductionism, the usual methodology of these gamblers, has often incorrectly carried the implication of an arrogant presumption of knowledge. Although a large majority of my colleagues hold the view, as did Jacques Loeb, that phenomena of biology obey the laws of physics and chemistry, and attempt to analyze many of these phenomena in these terms, I do not know any who believe that physiological phenomena are entirely interpretable with our presently available knowledge. However, to many of Loeb's contemporaries, descriptive morphologists at the end of the nineteenth century, the search for manipulable simple systems as an approach to generalizing biological laws may have seemed an affront to the then obvious complexity of the biological world.

At present the practitioners of this methodology will say only that they are following both the biologists, who, in the words of F. G. Hopkins "know best the lay of the land" and the chemists (and physicists) who have devised ever more penetrating exploitative techniques. Despite an interest in performing ever more sophisticated and elegantly controlled experiments, most investigators, even today, are enthused by the possibility of the unexpected, *i.e.,* a serendipitous discovery. In this sense, the poker game, replete with wild cards, may be merely the reflection of the aspirations of some well-known experimentalists.

In my recent examination of the early history of physiology, embryology, and biochemistry at the MBL, I have also turned up some unsuspected wild cards, which appear to challenge some current notions about our predecessors.

George Sarton has told us that a historian of science should know both history and science, and this ideal has proven to be quite difficult to realize. In the occasional mixed symposia of historians and scientists, these groups have tended to focus on different aspects of a problem under consideration and most often have talked past each other. In addition the two groups have developed a certain tension between them. The historians are suspicious of the personal involvement of the practitioners with the subject matter and other possibly related long forgotten events, while the scientists point to the neglect or lack of understanding of the scientific qualities of the problems by the historians. In my recent studies, it has appeared to me that an interplay of scientific and historical knowledge is essential in permitting a realistic look at the evolution of physiology at the MBL. It is not really possible to understand the growth of the discipline at that institution without a close study of almost all of the actors and their scientific problems, as well as their interactions on matters of personal, scientific, and institutional concern.

Whitman, Loeb, and Physiology

In examining the records of the MBL, the name of Jacques Loeb appears very early in the introduction of physiology at the Laboratory. A course of work in physiology as such was not introduced "for lack of space" in 1888, the first year of the opening of the laboratory (Whitman 1892). Whitman called attention to this deficiency in 1891 and acted to correct it in 1892. In his Annual Report of 1892, he stated that

> Morphology and physiology are two quite distinct sides of biology, each with definite and constant peculiarities of method and aim; but these two sides are only the statical and the dynamical aspect of one and the same thing; one presents the *feature* the other the *expression.* It is only as a matter of convenience that these two aspects are dealt with separately; they are complemental and have their full meaning only when united.

Whitman continued by insisting that the two sides be "kept in working contact." Separation has kept "physiology too exclusively in the service of Medicine" . . . "*The biological economy of organisms* must become an integral part of physiology." Both branches relate to problems of both evolution and development, *i.e.,* to paleontology and embryology, and "the history of morphology and physiology is one continuous illustration of their interdependence," as exemplified by Harvey's discovery of the circulation of the blood. There has been a "lack of interest in general physiology" and in marine biology. "It has been our good fortune to draw into connection with the Laboratory Dr. Loeb, whose enthusiasm, zeal, and accomplishments in general physiology, make him a fitting director of this department."

After a year at Bryn Mawr in 1891, Loeb was recruited by Whitman to the University of Chicago in 1892. Whitman's plan for the growth of an academic

biology that reflected the natural world rather than that of medicine called for a man of Loeb's broader interests at both his University Department and the MBL.

In the summer of 1892 Loeb began in a new building at the MBL, and worked with three postdoctoral associates and a number of students in a course of lectures and experimental studies. He soon became interested in embryological studies and reportedly was the first to perform experiments on the eggs of the sea urchin, *Arbacia punctulata* (Harvey, 1956). His paper described effects of hypertonic sea water on nuclear division without cell division (Loeb, 1892). T. H. Morgan, also working at the MBL, published on the same subject a year later (Morgan, 1893). It is of interest that at the MBL both of these men, who had had some administrative differences as fellow faculty members at Bryn Mawr, were pursuing similar problems in physiological morphology, *i.e.*, embryological development, on the same biological system. Although frequently differing in their conclusions, these men did respect each other's work, and had similar orientations to the major biological problems of the day. Both eventually left this complex but apparently confusing embryological system for more manageable materials, and as we know, both made fundamental contributions to quantitative biology. Morgan became an innovator of genetics and the theory of the gene, while Loeb can be considered to be a founding father of the physical chemistry of proteins. An important book on the latter subject (Cohn and Edsall, 1943) is dedicated to the memory of Jacques Loeb (1859–1924), in addition to tributes to Sir William Bate Hardy (1864–1934), Thomas Burr Osborne (1859–1929), and Søren Peter Lauritz Sørensen (1868–1939). The inscription in this volume of Cohn and Edsall reads "Their investigations laid the foundations for the physical chemistry of proteins."

Looking at Loeb and His Associates

Any working biochemist trained in the 1930's and 1940's would have many ties to Loeb. Taking courses in General Physiology and Colloid Chemistry in the 30's, one would have learned that, as a result of Loeb's work, the alleged distinctions between crystalloids and colloids, as applied to protoplasmic constituents, were spurious. He had shown that proteins combine stoichiometrically with acids and alkalis as a function of the hydrogen ion concentration (pH) and reactive ionizable groups on the proteins (Loeb, 1924). As a result, proteins may be soluble at one pH and aggregated at another. This manipulation was fundamental in the extraordinary isolation and crystallization of many proteins and enzymes in the late twenties, thirties, and forties by John Northrop and Moses Kunitz, both of whom had been close associates of Loeb at the Rockefeller Institute. Also, in another important branch of protein chemistry, the productive laboratory of E. J. Cohn during World War II used the physical chemical methods pioneered by Loeb to prepare many medically useful fractions of blood plasma. Loeb is an important figure to a biochemist of my period, and it was fascinating to learn that his biochemical discoveries began at the MBL with experiments on sea urchin eggs and hypertonic sea water.

Loeb's Early Research at the MBL

Several historians have outlined Loeb's early life as student and post-doctoral research associate in Germany (Fleming 1973; Pauly, 1980). His initial interest in the localization of brain function raised questions on the control of locomotion and animal behavior, subjects which led to studies of various tropisms. He then opposed the concept of instinctual behavior and objected to the use of psychological terms in describing biological reality. In the late 1880's Loeb had discussed problems of

plant motion with Julius Sachs who had wished "to reduce to chemistry and physics those functions amenable to such explanations" and had pointed to the effects of osmotic pressure and salts on plants (Pauly, 1980). As described by Pauly, Loeb saw science, and particularly biological science, as part of a human effort to cope more effectively with the environment. Going to the Stazione Zoologica in Naples in 1889 and 1890, he began to study regeneration and the creation of new animal forms in marine organisms.

Loeb's marriage to an American in 1890, his evaluation of his potential career in medically oriented Germany, and his friendship in Naples with Americans, such as Christian Herter, eased his decision to emigrate and to accept the offer of a position at Bryn Mawr. His move to the larger world of the newly established University of Chicago and an association with the enlightened and dynamic Whitman permitted him to become a virtually instantaneous leader of physiology in an America in which the discipline scarcely existed. It must be noted that Darwinian evolution in this pre-Mendelian era could offer no scientific proof of the mechanism of the origin of species and variation, and Loeb, as well as Morgan, were far from convinced at this time of the validity of "evolutionism." It has been suggested by Pauly that Whitman hoped research by Loeb and the physiologists would contribute to knowledge of the evolution of physiological function, whereas Loeb was interested primarily in the control of known function.

In any case, Loeb's research began at the MBL with the effects of hypertonic media on fertilized sea urchin eggs, and he believed he had detected nuclear cleavage without cellular cleavage (Loeb, 1892), a result which was challenged (Morgan, 1893). With the cytological aid of W. W. Norman of Texas, an associate in the Physiology Course at the MBL and previously at the Naples Laboratory (Norman, 1896), Loeb was proved correct and proceeded to exploit the observation of Morgan who had seen that salts produced mitosis-like effects in unfertilized eggs. By 1899 Loeb had discovered and reported "the artificial producton of normal larvae (plutei) from unfertilized eggs of the sea urchin" (Loeb, 1899). Loeb had indeed begun to "control" biological systems. In the summer of 1900, this result was confirmed by many workers and the cytology of parthenogenetic development of these eggs had been clarified (Wilson, 1901).

It should be evident that this surprising and dramatic feat was the consequence of many lines of work. Loeb, Sachs, and others had rejected the medical direction of German biology and had sought ever more controllable model systems. The Naples laboratory had helped to educate Whitman, Loeb, Morgan, and Norman in the importance of marine systems. Whitman's vision, energies, and administrative skills had built the MBL and the Department at Chicago, and had recruited Loeb. The personal qualities and interplay of all of these men had also contributed crucially. Nevertheless the induction of nuclear cleavage to artificial parthenogenesis had taken seven years of determined effort to answer Morgan and to go on from there. The need of a working scientist to define the nature of a possible mistake and to correct it, if necessary, can be a powerful driving force, and perhaps has not been considered sufficiently in analyzing the mainsprings of discovery. In looking at Loeb's career, we shall see that Loeb worked very hard and long to answer criticisms of his scientific results and conclusions. The nature of that need is not easily clarified.

A. P. Mathews, the Wild Card

In 1895, E. B. Wilson and Albert Prescott Mathews, the latter a student at Columbia University, made an interesting contribution to the study of the development of the sea urchin egg (Wilson and Mathews, 1895). Mathews spent a year

in Germany with Albrecht Kossel on the chemistry of sperm and in 1898 he completed his doctoral dissertation at Columbia on "The Physiology of Secretion" (Harvey, 1958). Having studied the chemistry of staining and the structure of cells of the pancreas, and with biochemical, cytological, and embryological training, Mathews, now Assistant Professor of Physiology at Tuft's College, joined the MBL faculty of the Department of General and Comparative Physiology in 1899 with Loeb and E. P. Lyon, Instructor in Biology of the Bradley Institute of Technology of Peoria, Illinois. Norman appears to drop from the course after 1898. This is the important summer of Loeb's great discovery, but in 1900 Mathews announced that quite independently he had caused cell division in unfertilized *Arbacia* eggs by anaerobiosis, heat and ether, alcohol, and chloroform. He also added that Morgan had conducted the first fruitful experiments on chemical ferilization in 1898, and that Loeb had confirmed and extended Morgan's work in 1899. According to Mathews, Loeb had been incorrect initially in his interpretations, but had now modified his views.

In 1901 (Mathews, 1901) Mathews published from Harvard on secretion, and on the effects of salts in the conductivity of the nerve. In another paper we learn more of artificial parthenogenesis, in this instance of starfish eggs, produced by mechanical agitation. This paper also included a confirmation attributed to Morgan, as well as unpublished data by Loeb on *Chaetopterus* and *Nereis*. It may be mentioned that embryologists, including E. E. Just, thought that this effect of shaking was due to the carbon dioxide or acidity generated in unduly concentrated suspensions of eggs.

In 1901 Mathews came to the University of Chicago in the Department of Physiology. He informed his brother, a newspaper reporter, of exciting unpublished work from Loeb's laboratory, which was then sensationalized in the press (Pauly, 1980; Kohler, 1982). Loeb was upset, and writing to President Harper, stated that Mathews should not have confiscated Loeb's unpublished work or have claimed that of Loeb's students, that Mathews' work was unsound "and of such a character as to sooner or later injure the reputation of the University" (Kohler, 1982). Kohler has also recorded some independent opinions casting aspersions on Mathews' scientific judgement. The resulting brouhaha led to the development of a "Code of Scientific Ethics" by the faculty of the University of Chicago (Pauly, 1980). By 1903 Loeb had left the University of Chicago for the University of California, but Mathews remained in Chicago and developed work in chemical biology, rising to the rank of full professor by 1905 (Kohler, 1982). He left Chicago only to go to the University of Cincinnati where he began a program in clinical chemistry.

In long papers in *Science* on nerve stimulation, Mathews turned his attention to physical chemistry, attempted to correct some of his own initial mistakes in attributing salt effects to the production of hydroxyl ions, and then enlarged upon new results correcting errors assigned to Loeb (Mathews, 1902). When Loeb responded criticizing some of Mathew's notions, such as those of stimulation and inhibition being due to a precipitation and resolution of nerve colloids respectively, Mathews continued at length, and introduced new speculations on his results with eggs, kidneys, and central nervous system (Mathews, 1903).

Loeb now had a large number of criticisms and claims to which to respond. In fact, although far more circumspect than Mathews in referring to his antagonist by name, Loeb did continue to explore the matters raised by Mathews and eventually responded to many of them. For example in 1899 Loeb had reported that calcium ion inhibited muscle twitching caused by NaCl and had suggested that stimulation by citrate, oxalate, fluoride, and phosphate might be due to precipitation or other binding of calcium. On the other hand Mathews expressed the belief in 1903 that

only anions are stimulating and that cations are depressing. Exploring the effects of salts of ammonium and tetraethyl ammonium ions and other amines, and a large array of other salts Loeb and Ewald showed in 1916 that calcium "does not inhibit the efficiency of the stimulating salt by depressing the irritability of the nerve." Many other facts are adduced and in conclusion "All these facts contradict the hypothesis of Mathews. . . ." (Loeb and Ewald, 1916).

Loeb's continuing concern with Mathews' counter hypotheses can be found in some of his later papers (Loeb, 1914a). It may be asked if his almost exclusive concentration on salt effects and ion binding in his later experimental years did not result in significant measure from the knowledge he had developed in responding to these old criticisms. Loeb's initial formulation of the idea that ion effects on protoplasm were interpretable by the laws of chemistry and physics was stated as early as 1904, and his criticisms of the proposed differences between colloidal and crystalloidal proteins sharpened as his studies on ion binding became more rigorous.

The existence of this deep personal and professional antagonism between Loeb and Mathews raises many questions concerning Mathews' position at Chicago and at the MBL. How did he manage to remain at Chicago? Mathews led the MBL physiology course after Loeb's departure for the University of California in 1903, and remained associated with it until 1919. Indeed he was elected a Trustee of the MBL in 1906 and remained a Trustee, even if emeritus, until his death in 1957 (Harvey, 1958). When Loeb left California for the Rockefeller Institute in 1910, he spent his summers at the Institute laboratory at the MBL, with associates among whom were Northrop and Kunitz. He also was a Trustee until his death in 1924. It might be imagined that Mathews and Loeb might have had quite divergent opinions on the organization of the physiology course, and might well have expressed these. However there is no significant mention of Mathews in the minutes of the Trustees and of the Executive Committee of the Trustees. The minutes and formal reports are models of tact, obscuring the tensions of the times.

The Manning-Just-Loeb Connection

As indicated earlier, a career in biochemistry and cell physiology does sensitize one to the name of Jacques Loeb. In addition a literary event in 1983 has most forcefully brought Loeb to our attention. The biography of the Negro biologist, Ernest Everett Just, written by the black historian, K. R. Manning (Manning, 1983), was widely and favorably reviewed this past year. The book describes the social and institutional difficulties of a black biologist in America from 1910 through 1940. Woods Hole and the MBL are portrayed as a somewhat racist community and institution respectively, in which the apprentice Just earned his keep by menial labor and was trained to do research by the Director, F. R. Lillie. Just eventually obtained a doctoral degree under Lillie at the University of Chicago and worked independently at the MBL on problems of embryological development. Although Just had risen to a Professorship at Howard University, had published extensively with Lillie, and was recognized as quite knowledgeable in his field, he was unable to obtain a position in a major white University, and indeed he had been warned of this on many occasions by his teacher and adviser, Lillie. He had indeed failed to "break out" of Howard to a more respected position, and was unable to make a "lasting psychological adjustment" to his predicament. Although recognized as a great Negro biologist, he wished desperately to be recognized as a great biologist. In describing Just's failures, Manning's book imputes racist behavior to the Jew, Loeb, dubs Abraham Flexner, a "paternalistic segregationist," and dwells gratuitously on the unpleasant personal reputations of some Jewish physiologists. Just is quoted as

having written in an appeal to Lady Astor in the 1930's that he had been "put in the bad book by Jews generally."

However throughout the book one finds that Loeb had helped Just considerably on several occasions early in his professional career, that Flexner had assisted Just often through various philanthropic agencies, and that Just had obtained warm, even caring personal support from some Jewish colleagues and friends. Nevertheless one is left with the claim that Loeb was a major factor in the tragedy of Just.

It is appropriate to consider the evidence that Loeb was a racist because Manning has not discussed the succession of events in the context of the interactions of scientists who disagreed publicly as well as privately on matters of science. Some of the weaknesses of Manning's arguments may be summarized as follows:

(1) Since 1904, Loeb had abandoned the mystique of colloidal chemistry which was retained by Just, Mathews, and close colleagues of Just such as L. V. Heilbrunn through the late 1930s. This neglect of scientific differences will be considered in more detail below.

(2) The twenty-year-old relations of Just to his teacher and adviser Mathews are discussed without reference to the unfriendly relations of Mathews and Loeb described above.

(3) Loeb's antiracist publications in 1914 (Loeb, 1914b) are not quoted, but he is rebuked for not having made speeches at NAACP meetings.

(4) In a letter to a Flexner, Loeb is known to have objected to Just as a possible colleague at the Rockefeller Institute. Just is stated to be "incompetent." The referencing is confused, and the exact quotations are distorted (Manning, 1983). In any case, Loeb believed that Just "was one of the men who were making Woods Hole an impossible place for a decent scientist to live in" (Pauly, 1980). If read carefully, this might be interpreted to indicate that Just is only one of numerous miscreants at the MBL, and this could not be an argument on racial grounds. The suggestion that Just would be better off as a high school teacher is also suggested to be racially motivated. None of these inferences are discussed in the context that Just had been denouncing Loeb's science in print and at meetings for some years.

(5) Despite such attacks by Just against Loeb, the latter is expected to have supported Just's appointment at the Rockefeller Institute, as "symbolic for the whole black race" (Manning, 1983). Manning, the historian, is calling for "affirmative action" in 1923 from Loeb, who has been publicly criticized by Just.

(6) Commenting on Loeb's scientific disagreements with Lillie, the most important of Just's teachers, advisers and collaborators, Manning suggests that Loeb founded the *Journal of General Physiology* in part to block Lillie from publishing (Manning, 1983). John Northrop's memory of Loeb's impatience in publishing in previously existing journals seems far more convincing (Pauly, 1980).

There does not appear to be direct evidence of racism on Loeb's part. It should also be noted that Just's alienation from American society continued and exacerbated long after Loeb's death in 1924.

The Mathews-Just Connection

The point is made by Manning that Just's attacks on Loeb are often attributable to Just's loyalty to his teacher and adviser, Lillie, whose scientific outlook and analyses differed from those of Loeb. It is relevant to note that A. P. Mathews was also teacher, friend, and scientific adviser to Just and that Loeb's attitude to Just may also have been influenced by the other protracted war between Loeb and Mathews described earlier.

When Just studied at the University of Chicgo in the academic year of 1914–15 to fulfill his residency requirement for the doctorate, he took a course in cell chemistry with Mathews (Manning, 1983). Mathews has been quoted to the effect that Just was "better than any other student in the class," and likely to become "one of the most original and creative men in zoology in the United States." Their association continued at the MBL and professionally through the late 1930's. In 1935, Mathews encouraged Just to express his controversial opinions challenging current genetic theory at a meeting of the American Society of Zoologists, and to emulate Lavoisier's revolution in 18th century chemistry (Manning, 1983).

A. P. Mathews is credited with having written the first American textbook in biochemistry in 1915. It was written for medical students, was quite popular, and went through six editions, of which the last was in 1936 (Mathews, 1936). It was said to have irritated colleagues with personal asides, among other non-standard components (Kohler, 1982). Mathews' style was apparently consistent. The 1915 book has been described (Chittenden, 1930) as comprehensive, critical and valuable. Chittenden's evaluation of Mathews' contributions comments favorably on a discovery of the spontaneous oxidation of sugars and cysteine in alkaline solution but notes his work on protein precipitation by ions without other comment.

However Florkin did comment unfavorably on the 1924 edition of Mathews' book in a chapter on "The Dark Age of Biocolloidology" (Florkin, 1972). Mathews was quoted as follows:

> It is by means of the colloids of a protein, lipoid or carbohydrate nature, which make up the substratum of the cell that this localization of chemical reactions is produced; the colloids furnish the basis for the organization or machinery of the cell; and in their absence there could be nothing more than a homogeneous conglomeration of reactions. . . . The colloids localize the cell reactions and furnish the physical basis of its physiology; they form the "cell machinery."

In 1936, long after the important work of Loeb, Adair, and Svedberg in 1924, Mathews' text was still describing as uncertain the molecularity of hemoglobin and other defined proteins (Mathews, 1936). Unfortunately, Just's orientation to cell chemistry in 1939, the year of publication of his book *The Biology of the Cell Surface* (Just, 1939a) which was to make his final statement, was essentially still that of the colloidal chemistry of his teacher and even recent adviser, A. P. Mathews. It was unfortunate that Just, focussing on the potential roles of cell membrane and the underlying cytoplasm, which he termed "ectoplasm," died in 1941, before the power of electron microscopy became known and available and before the underlying nucleoprotein particles in cytoplasm had been described by Caspersson and isolated and analyzed by Brachet and Claude. Just's book, published just before World War II, could not have received active attention by either the Europeans at war, or the increasingly distracted Americans.

Was Loeb Wrong About Just?

Loeb and others considered Just to be arrogant, conceited, and boastful in his aggressive claims for recognition of achievement (Manning, 1983). However it is probable that Just felt it necessary to assert himself more forthrightly than is customary in obtaining recognition by his peers. What is peer review for a black biologist?

Of the three groups with which Just had been associated at the MBL, all of whom had studied the embryological development of marine eggs, only Just had

stayed with the problem and had come to a sense of the importance of cytoplasm. T. H. Morgan, after confusing starts and shifts, had dropped the problem and had focused on mutations in *Drosophila;* his work in genetics culminated in a Nobel prize. Loeb also had dropped the problem and in attempting to understand his earliest work had become both a founding father of protein chemistry and a legend, depicted in part in "Arrowsmith." Lillie, with whose research work Just had been associated for years, had become President of the National Academy of Sciences. Meanwhile embryological work had demonstrated that egg fragments lacking nuclei and genes could develop after fertilization, or even divide after stimulation without fertilization. Just emphasized the importance of the cytoplasm, as had Morgan earlier, but finally had overreached himself (Just, 1939b) with unnecessary attacks on genetics (Manning, 1983) and extreme theories on the nature of the cellular division of labor.

However it may be noted that in November 1936 Just wrote to Lillie from Howard University, described his most recent work, and requested that Lillie write to support another request for financial help.

"Whilst as you would appreciate my interest is in the biology, I have had to go into the chemical end of the nucleoproteins. In this I have had great help from Dr. A. P. Mathews. He has also written a very strong letter in my behalf. . . ." (Just, 1936). Later in Just's "Status of my research program in embryology . . ." to Lillie, apparently written in 1939, he states "as a law that differentiation during development never appears without attendant progressive synthesis of nucleoprotein" (Just, 1939b). Believing the increase of nuclear substance to be effected in the cytoplasm he proposes

> a more exact study of nucleo-protein synthesis to embrace as many different types of eggs as possible. . . . My measurements, up to now as rough as those of others who had made such, I can refine. The aim here is to follow by careful observation and experiment the moment to moment changes in the cytoplasm as the nuclei are built up, to correlate them with nuclear synthesis and thus to derive a biological law of general validity for all cells undergoing differentiation.

Could the aging biologist, Just, have learned these techniques? Could he have determined that DNA is not synthesized in the cytoplasm and then have learned more about the division of labor within cells? Could he, like Loeb and Morgan, have achieved genuinely important contributions to our understanding of cellular biology relatively late in life? We cannot know, but understand that his thread of an idea might have become the rope on which he might have climbed into the modern cellular science of the post-war world.

Closing Remarks

A look at the newly assembled Archives at the MBL reveals old data and new questions. How did these perpetually quibbling, quarreling, or warring scientists live together, experiment, and survive and grow professionally? How had Woods Hole in 1923 become an impossible place for a decent scientist to live in? And what was a decent scientist? Will we be able to develop historians of biology who will know enough history and enough science, as well as a few other essential disciplines?

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THE ZOOLOGICAL STATION AT NAPLES AND THE NEURON: PERSONALITIES AND ENCOUNTERS IN A UNIQUE INSTITUTION

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Introduction

When the young Dozent of Comparative Anatomy at the University of Jena, Dr. Anton Dohrn, became obsessed with the idea of building a Zoological Laboratory on the shores of the Mediterranean Sea at Naples, his enthusiasm was riding the crest of a wave of excitement that had spread throughout Europe and eventually reached the North American continent. It was the excitement generated by Darwin's new theory of evolution which was so infectious because it reinforced the new tendency towards a rational and mechanistic explanation of life phenomena that had already been in full development.

The science of Zoology had only recently been established. Only five years earlier, in 1865, Ernst Haeckel had been appointed professor of Zoology at the University of Jena on the recommendation of the great Karl Gegenbaur, then professor of Anatomy and Zoology at the same university, and was provided with a new Zoological Institute. This was the year in which Anton Dohrn received his Ph.D. degree at the University of Breslau under Eduard Adolf Grube (who had been appointed Professor of Zoology there in 1857). Dohrn had studied under Haeckel in 1862, after Haeckel had just become Extraordinarius of Comparative Anatomy in Gegenbaur's institute. In 1868, Dohrn became Privatdozent of Zoology in Jena, but later, in the same year we find him already in England and Scotland, and in 1869 at Messina in southern Italy, carrying out embryological studies on marine organisms. What a restless character he must have been: while a student, he changed universities five times! From the University of Königsberg he went to Bonn, then to Jena, moved to Berlin, and finally received his degree at Breslau. He was indeed a man of action: within a span of only three years after his return from Messina he had established the Zoological Station at Naples which opened its doors in 1873! It must be remembered, however, that at that time the Zoological Station was not yet the international institution it was to become. The Stazione Zoologica was built with Dohrn's private funds. Indeed, the contract with the city of Naples which granted him the right to use the land on which he had built his institute was signed, but two years later. All along it had been Dohrn's intention, however, to offer the services of his institute to scientists from all countries. To make this possible he sought, and obtained, on the recommendations of some of the most important scientists of his time, funds from scientific institutions and governments of many countries to whom he "rented" research facilities: the so-called "tables."

From the beginning Dohrn regarded Zoology as an experimental science and saw the main thrust in the development of morphology, embryology, and physiology. He seized the newly won status of zoology which he described so emphatically in his programmatic paper on "the present state of Zoology and the founding of zoological stations" which appeared in the *Preussische Jahrbücher* (vol. 30) in 1872:

> When thus Zoology with all its branches has acquired new stature and importance, it is not surprising that in zoological circles everyone labors with redoubled

> energy. As after a great victory the members of the victorious nation appear among the other nations with elated selfconfidence and are—albeit grudgingly—regarded by them with increased respect, so appear the Zoologists in the midst of the other scholars in the full consciousness that it is their science that has developed and brought to maturity the greatest concept of modern research, and that it is their task to nurse and extend it, and that the other sciences must receive it and must be fertilized and reformed by it.

In this important publication, Dohrn spelled out the new goals of Zoology: to study the basis of natural selection (*natürliche Züchtung*) and to investigate the evolutionary origins of animal adaptation to the environment. Dohrn envisions an ecologically oriented comparative physiology and emphasizes the need to explain organ functions on the basis of adaptation and evolutionary history. The foundation of zoological stations should provide the ideal places where such a science could be developed.

Dohrn saw, however, another important task in the foundation of marine stations: the opportunities they offer for the rising generation of zoologists. He wanted to provide promising young zoologists with the freedom to carry out research in the most conducive environment a zoologist can find, and to free them from financial worries for the time of their stay at the zoological station.

Fridtjof Nansen: The Structure of the Nervous System

The motivation to encourage and support promising young zoologists must have prompted Dohrn to accept, in 1886, a young Norwegian zoologist by the name of Fridtjof Nansen as a guest of the Stazione Zoologica, at a time when neither Norway, nor any of the other Scandinavian countries had reached financial agreements with the Zoological Station. Nansen was keenly interested in a problem that engaged both physiologists and histologists in heated debates: the relationship between ganglion cells and nerve fibers, the nature of the nervous impulse and the cellular basis of the functioning of the brain. Nansen had been led to these questions through his investigation of a class of parasitic annelids, the myzostomids. When he studied the histology of their nervous system he found himself confronted with this fundamental issue and had to discover that the existing research literature could not help to resolve it. He felt impelled to carry out comparative studies.

Nansen has become famous not for his work in zoology, or neurohistology, but for his exploration of the arctic. With Sverdrup he crossed Greenland (two years after his stay at Naples), and from 1890 to 1896 he carried out his exploration of the north pole. As high commissioner of the League of Nations he introduced (in 1921) the famous Nansen-passport, and in 1922 he received the Nobel peace prize. His earlier accomplishments as a scientist and explorer have been recorded in a very readable biography by W. C. Broegger and Nordahl Rolfsen: "Fridtjof Nansen 1861–1893" (1896). This book contains a 22-page chapter entitled "In Naples" which describes, partly in Nansen's own words (quoted from his 1887 article in *Naturen*), the Zoological Station and the great impression Anton Dohrn made upon the receptive mind of the young Nansen.

Nansen, then Curator at the Museum of Natural History at Bergen, Norway, was only 25 years old when he came to Naples. He was dissatisfied with the prevalent histological techniques then available for the study of the structure of the nervous system. He was open-minded enough to recognize the great potential of the new staining method invented and developed by Camillo Golgi at Pavia. A born explorer, he immediately set out to travel to Pavia to get first-hand knowledge of the new method. In 1885 Nansen had won the Joachim Friele gold medal for

FIGURE 1. Fridtjof Nansen sent this portrait to Anton Dohrn. On its back he wrote the following dedication: "Dem Herrn Prof. Dr. A. Dohrn mit vorzüglicher Hochachtung zur freundlichen Erinnerung von Fridjof Nansen Bergen 3. April 1887" (Private archive of the Dohrn Family).

his work on that peculiar class of annelid worms, the Myzostoma (today known as Myzostomida). He accepted the medal in copper and used the value of the gold for his traveling expenses. After a short stay at Pavia he continued to Naples where he was assigned a working space in a large upstairs laboratory already occupied by five other scientists. The Zoological Station had already been open for a dozen years. Numerous countries supported it in exchange for the right to one or more "research tables" for their respective scientists. Norway at that time did not yet participate, and it was due to the generosity of the director of the Statione Zoologica that Nansen was given the opportunity to spend two months at this institution. Upon his return to Norway, Nansen published an article on the Zoological Station in the Norwegian popular science magazine *Naturen.* Excerpts can be found, in English translation, in Brögger and Rolfsen's Nansen Biography of 1896. Nansen's enthusiasm for Anton Dohrn's work and achievements can be gleaned from these quotations:

> The whole basement of the great building is fitted up as an aquarium for the general public; an aquarium which it would certainly be difficult to rival. This great room, with its many tanks, is soberly decorated, with a complete avoidance of all humbug [sic] or fantastic ornament, which would only serve to distract the attention from its essential purposes. It has a great attraction not only for the ordinary traveller, but for the scientific student as well. Down here he is able to pass hours in communion with nature, and face to face with the rarest of marine organisms, and in a comparatively brief time he may learn more of the life of the world than he could by long grubbing in volumes of printed wisdom, or rooting through the dead treasures of museums. He will contract the habit of using his eyes and of his powers of observation upon living nature, and learn to regard life as the essential object of research.
>
> Acquaintance with the Station, for the majority of tourists, does not extend beyond this room. Far more important to science, however, are the laboratories situated in the upper stories of the building. Here naturalists from almost all European countries are at work, here they have everything they can possibly require for their studies. They can come to the Station, sit down at the work-table assigned to them, tell the Curator, Salvatore Lo Bianco, what particular animals they want, and presently the animals are brought alive to their very tables, where they can study them at leisure, with no need to stir from their places except for meals and sleep. Instruments, smaller tanks in which to keep the animals alive, and an excellent library, are all just at hand. This concentration of appliances is the novel and important feature of the institution. . . . If the workers are tired of the laboratory, they are free to go out in the vessels belonging to the Station, and watch the gathering in of fresh specimens. Beside several fishing boats, the Station owns two small steamers. . . . These steamers and boats are equipped for dredging, trawling, net-fishing, surface-fishing, and so forth. They are also supplied with diving apparatus, so that in this way, too, you can fetch up whatever you want.

What was it that Nansen wanted to accomplish at Naples; what actually did he accomplish? When his biographer W. C. Brögger inquired of Anton Dohrn what he remembered of Nansen's stay in his laboratory, Dohrn felt somewhat embarrassed that he could not be of much assistance; all he could recall was that Nansen was working "mainly on *Amphioxus* and on *Selachians,* making use of the new Golgi method." Dohrn recalled, however, that Nansen was "a smart dancer, who certainly did not disdain the company of lively ladies. I believe not to err when I report to you that a beautiful Scottswoman competed dangerously with his studies and presumably was the cause of his exchanging Naples for Rome earlier than he had originally intended."

In actual fact, Nansen had used his time very well indeed. Of course, the research he did at Naples was only a part of a wider ranging endeavor. He continued his comparative studies on the nervous system in Bergen where he also received from Naples more specimens of *Amphioxus,* "most excellently prepared in different ways by Salvatore Lo'Bianco." Already at Naples he had immersed himself in a thorough study of the research literature. It seems incredible that already in 1887, only one year after his return from Naples, where, after all, he had spent only two months, Nansen published a 214-page monograph with 11 plates, entitled *The Structure and Combination of the Histological Elements of the Central Nervous System.* Fully 80 pages of the monograph are devoted to the history of the subject. His literature list is respectable and amounts to no less than 21 pages. In this very illuminating account of the research of others and of his own, Nansen reaches conclusions about the general structure and function of nervous systems. Because he investigates ganglion cells mostly in invertebrates, and studies only the spinal ganglion cells of vertebrates, he assumes that ganglion cells have mainly a nutritive function. He correctly interprets the nature of what Franz Leydig had called the "*Punktsubstanz,*" and what later became to be known as the neuropil, as being composed of innumerable fine nerve branches. He also correctly interprets the course of nervous excitation during reflex actions. As to the connections between ganglion cells and nerve fibers he is somewhat ambiguous but favors the view that nerve fibers are outgrowths of ganglion cells.

It may seem surprising that Nansen does not once mention the work and ideas of Anton Dohrn on the subject, but Dohrn's research on the nature of nerve cells and ganglion cells had not yet advanced to the stage of publication, and the subject may never have come up in conversation between these two men. There was, however, an Hungarian neurohistologist working at the Zoological Station who certainly influenced greatly the thinking of Anton Dohrn, and who also was well acquainted with Fridtjof Nansen. He was Stephan von Apathy from Koloszvar. Apathy had developed a staining method involving gold-chloride, formic acid, methylene blue, and hematein, which permitted the demonstration of a "*Fibrillengitter:*" ganglion cells and nerve fibers were shown to contain fibrils. Apathy's preparations seemed to indicate that these fibrils formed a continuous network throughout the nervous system. The fibrils were seen to cross from one cell process to the next at their contact points. Apathy considered these fibrils to be the true conducting structures of the nervous system. Apathy was indeed an excellent histologist, and his superb preparations convinced and influenced many of the leading histologists, among them Wilhelm His, Franz Nissl, Max Bielschowsky, and Hans Held.

That it should have been possible to subscribe to the notion that the neurofibrils (to use a modern term) are the "conducting elements" of the nervous system is almost incredible when one remembers that electrophysiologists (Du Bois-Reymond, Hermann, Bernstein) had long before established the electrical nature of the nerve impulse: it would have been inconceivable to the biophysically trained physiologists that separate action currents can be conducted within a given nerve cell or even within a nerve process. Evidently, electrophysiology (today this would be called biophysics) was not taken that seriously by the histologists, and even a physiologist like Albrecht Bethe became so impressed by Apathy's results that he was willing to accept the hypothesis that the fibrils and not the nerve fibers are the true elements (or 'units' as we would say today) of the nervous system.

In their Nansen biography, Brögger and Rolfsen (1896) quote a letter evidently written to them by Apathy, who reminisces about the life he and others shared with

Nansen while they were at Naples. "One of these friends, a Hungarian scientist," they state,

> writes to us: 'He was the life of all our little festivities. Most of the students then working at the Station were in the habit of meeting at the Cafe Basta on the Corso Vittoriao Emmanuele; every evening at suppertime there was a little feast here, a musical gathering, light-hearted and refreshing in the highest degree. Nansen contributed greatly to the prevailing gaiety. It some times happened that we devotees of science became so enlivened with wine and music, that we proceeded to dance a quadrille; and on these occasions Nansen was Master of Ceremonies.
>
> 'Once we chartered a carriage to drive to Castellamare and Sorrento by the famous coast road. On the way, another carriage with two ladies came up behind us. The ladies amused themselves by racing us and laughing at us as they shot past; whereupon Nansen sprang out of the carriage and ran by the side of the horse a long stretch of the way. Thus we overtook the ladies again, to the unbounded merriment of both parties.
>
> 'In Sorrento Nansen met some Norwegian ladies. I was very tired and went to bed; but the Norwegian ladies wanted to get up a dance, and as there was a scarcity of partners, my presence was required. Nansen declined to give a moment's peace till I got up and dressed myself. Then he dragged me into the drawing-room, where we were greeted with loud applause by the ladies, who were quite alive to the situation.
>
> 'At other times he would be quiet and absorbed, and would sit by the hour without uttering a word. I have seen him at the foot of Vesuvius, among the ruins of San Sebastiano, and on the melancholy lava-wastes. San Sebastiano was devasted by the eruption of 1874; nothing was left but a church. I have seen him sitting on a block of lava there by the church, hour after hour without stirring; he simply sat and gazed out into the distance. Time after time we others tried to make a start, and called to him—he never moved. Afterwards, on the way home, as he and I walked together, arm in arm, I tried to make him talk, but found him absolutely mute—there was not a word to be got out of him.'

Anton Dohrn: The Nerve Fiber

Before continuing with Stephan von Apathy and his impact through the Zoological Station at Naples, let me return once again to Anton Dohrn. With an immense effort, Dohrn occupied himself with his "Studien zur Urgeschichte des Wirbelthierkörpers" (Studies on the early history of the vertebrate body). As by a magnet he was drawn to the problem of the structure of the nervous system which he tried to resolve by studying lower vertebrates and their embryological development. It was a heroic effort of trying to understand the central nervous system of higher vertebrates on the basis of Haeckel's "biogenetic law," the notion that ontogeny recapitulates phylogeny and that any structure found in higher organisms must have its primitive counterpart in the earlier stages of evolution as represented in primitive animals. The question was, in Dohrn's words, "is the nerve fiber an outgrowth of the ganglion cell? or is it composed of numerous cells, the exponent of which can be regarded the Schwann nuclei?" Dohrn called the decision of this question "the foundation of our ideas about the nervous system." In the 16th of his "studies" he comes to the definite conclusion that the nerve fiber arises through the fusion of Schwann cells and that "the central ganglion cells have nothing to do with the beginning of the axis cylinder or the entire formation of the nerve fiber." Ganglion cell and nerve fiber are connected by contact, they are not genetically related. In his views, Dohrn finds himself supported by Apathy whom he quotes extensively.

Shortly after publication of his 16th "Studie" in 1891, Dohrn was plagued by doubts about the correctness of his interpretations. He rushed into print a retraction in the *Anatomischer Anzeiger* (vol. 7, p. 348). The famous Anatomist Albert Koelliker had announced a Lecture to be given at the Congress of Anatomists to be held in Munich with the ominous title "Ueber die Entwicklung der Elemente des Nervensystems, contra BEARD and DOHRN." Because of Dohrn's retraction, the actual lecture had the simpler title ". . . contra BEARD." Ten years later, Dohrn decided that he should not have retracted his views. His doubts, he said in his 20th "Studie," had been mainly "of subjective origin, and were due to a nervous depression caused by overwork, climatic and other influences, the like of which I unfortunately had to suffer repeatedly due to the abrasive work and the complicated conditions of life connected with my position as director of the Zoological Station" (p. 139, vol. 15 of the *Mitth. Zool. Stat. Neapel*, 1901).

It would be unfair to judge Anton Dohrn by his, by present standards, misguided endeavor to solve once and for all the enigma of the cellular relationship between ganglion cell and nerve fiber. Dohrn's vision was far more wide ranging, and truly important. He clearly saw the need to encourage the development of comparative physiology and biological chemistry, and he was able to generate interest in the enormous potential of a marine laboratory for the expansion of knowledge in this important area of experimental biology. Many of the important physiologists were attracted to the Zoological Station, among them Max Verworn, Sigmund Exner, Jaques Loeb, Willem v. Einthoven, and Jacob von Ueuxküll.

In 1906 Dohrn created, with newly acquired funds, departments for physiology and for physiological chemistry in the Zoological Station; he employed H. Burian and M. Henze as heads of these departments. Dohrn motivated Otto von Fürth to write the influential *Vergleichende chemische Physiologie niederer Tiere* (Jena, 1903), probably the first text of biological chemistry. There can be no doubt that it was due to the influence of Anton Dohrn and his Zoological Station that Winterstein was induced to publish the monumental *Handbuch der vergleichenden Physiologie* (published in eight volumes between 1911 and 1925, together no less than 9321 pages!): almost all of the authors had been working at the Zoological Station. Like this Station, the *Handbuch* was an international affair: the contributing authors hailed from eight different countries.

Already in the late 1890's, Hermann J. Jordan had been Dohrn's private assistant. Later, Jordan was to become one of the most influential comparative physiologists. On the recommendation of Jordan, T. H. Morgan appointed two of Jordan's pupils to important posts at the California Institute of Technology: C. A. G. Wiersma, and A. van Harreveld. The work of these great neurobiologists thus reflects the heritage of Anton Dohrn.

Albrecht Bethe: Ganglion Cell and Reflex

The neuron doctrine, enunciated by Wilhelm Waldeyer in his famous paper in the *Deutsche Medizinische Wochenschrift* of 1891, was welcomed by physiologists. But neurohistologists like Held, Nissl, and others, continued either to oppose it or to regard it with utmost caution. In 1896, Albrecht Bethe, a pupil of Goltz in Staßburg, later professor of Physiology at Frankfurt, came to Naples to study the nervous system of the shore crab, *Carcinus*. His goal was a complete histological and physiological description of the neurons in what he then considered to be a "simple nervous system." His encounter with Apathy forced him to completely revise his ideas about structure and function of nervous systems. In his important

book *Allgemeine Anatomie und Physiologie des Nervensystems,* published in 1903, Bethe writes that he had been skeptical at first of Apathy's papers:

> because of the aprioristic form in which they were written, and because of the peculiarity of the result which were suported either with no pictures at all, or with only schematic illustrations. My doubts disappeared rapidly, however, when Mr. von Apathy, on the occasion of our meeting at the Zoological Station at Naples in the Fall of 1896, had the kindness to show me his preparations. On the evening before this memorable day I had still told him that I considered what he had published outside of all possibilities, and that it must be due to self-deception when he thought that he could follow such fine fibrils individually for millimeters. What has been shown to me then, however, was of such convincing clarity, that I was forced, after some pretended objections, to relinquish my opposition. What happened to me was experienced by many others, and nobody of normal vision can elude the convincing impression of Apathy's preparations unless his eye is beclouded with envy or injured vanity.

As a consequence of his "conversion," Bethe looked at the nervous system as a syncytium. The ganglion cells were unnecessary to explain reflex actions, as he demonstrated by an experiment that henceforth would be known in the literature and in physiology texts as the "Bethe experiment." In Naples, working with *Carcinus,* Bethe did the following experiment: he removed the ganglion cells that surround the neuropil of the second antennae, severed the connections between this neuropil and the rest of the nervous system, and cut the esophageal commisures. He noted that the antennae still maintained their tonus and that they were held stiffly in their normal raised position. When mechanically stimulated the antennae were retracted, but afterwards were once again extended. From this experiment Bethe concluded that ganglion cells are either unnecessary for these reflexes to occur, or the reflex arcs do not go through the ganglion cells. As he was convinced now that it is the fibrils which serve as the connecting elements, he concluded that the "Primitivfibrillen" (the elementary fibrils of which the composite fibrils are composed) are the true conducting elements of the nervous system.

Bethe's experiment was widely quoted by those opposing the neuron doctrine. Indeed, Bethe himself declared "we must stop considering the neuron as a physiological unit and must admit that one and the same neuron is capable of many diverse actions, depending on which fibrillar tract is in operation."

The Zoological Station at Naples was indeed a cross-roads of the biological sciences. The meeting there between Apathy and Dohrn who became close friends, gave Dohrn the needed confidence that he was on the right track, that he had solved the riddle of the fundamental cellular nature of the vertebrate nervous system. Dohrn's work in turn gave affirmation, as did Apathy's work, to the many histologists (and physiologists) who opposed the neuron doctrine. The meeting of Apathy and Bethe led Bethe to completely reconsider his ideas about the structure and function of the nervous system. In 1893, Bethe had set out to completely describe the nervous system of what he considered to be a simple animal using neurohistological techniques as well as physiological experiments. He went to Naples with the express idea of "mapping the nervous system," of describing all its neurons and their interconnections—a task which has not been tried again until C. A. G. Wiersma began his pioneering studies of the central nervous system of crayfish in the late 1950's at the California Institute of Technology (see *Identified Neurons and Behavior of Arthropods,* edited by G. Hoyle, 1977). Bethe could have accomplished much of what neurobiologists started to do six decades later, had he not been discouraged by the histological findings of Apathy which he was able to confirm in

his own work on *Carcinus* carried out at Naples. It is touching to read the final passage of his third report on his *Carcinus* experiments which was published in 1998:

> When I began this work three years ago, I expected to advance with my knowledge of the anatomical structure of the Nervous system of *Carcinus* to a point where I could describe about all the nervous elements and their branches. After preliminary studies I considered their interconnections not to be too complicated, and I believed I should be able to clearly reveal the significance of each by physiological experiment. At that time it seemed that if this was achieved we would be very much closer to an understanding of the nervous system. The epochal work of Apathy has shaken this hope in its foundations.

It would now be necessary to discover the course of each single fibril—"and this is unthinkable. As I now overlook my whole work, I reach the sad conclusion that nothing has been gained from it for our factual knowledge. Were there not satisfaction in the search for knowledge, one would have to say in resignation: it is too difficult for us humans."

The "Bethe experiment" on *Carcinus* has been a stumbling block for the general acceptance of the neuron doctrine which holds that the axon is an outgrowth of a ganglion cell, that all nerve cells are ganglion cells (while Schwann cells like most other cells of the nervous system, are glia cells), and that each neuron is a separate unit which does not fuse anywhere with another cell, contacts being only in the nature of synapses. In 1909 the famous Otto Langendorff, writing in Nagel's authoritative *Handbuch der Physiologie des Menschen,* debates the Bethe experiment. He accepts Bethe's conclusions as valid for crustaceans but expresses the opinion that "reflexes of invertebrates are perhaps of a lower level," hence the neuron theory can still be valid for vertebrates. As late as 1927, another well known German physiologist, Emil Abderhalden, states in his textbook of Physiology (*Lehrbuch der Physiologie,* 1927, p. 115) that it is "an established fact" that the nervous system is constituted of cells which are interconnected by strands of fibrils. Bethe's experiment on *Carcinus* plays an important role in Abderhalden's arguments.

Stephan von Apathy: Neurofribrils

In the history of neurohistology, Stephan von Apathy has been of great importance. The major breakthrough was the development of new staining methods while he was working at the Stazione Zoologica at Naples. For three years (1886–1889) Apathy occupied the Hungarian "research table" at Naples. Anton Dohrn assigned to him the task of writing a monograph on the *Hirudinea* for the now famous *Fauna und Flora des Golfes von Neapel.* Both men became close friends. Apathy based much of his later speculations on the fine-structure of the nervous system on whole-mount preparations of the gastrointestinal tract of the marine leech *Pantobdella muricata.* His publications, especially his paper "Das leitende Element des Nervensystems und seine topographischen Beziehungen zu den Zellen," published in 1897 in the Zoological Station's "house journal," the then prestigious *Mittheilungen aus der Zoologischen Station zu Neapel* (vol. 12), generated excitement and heated debate among neurohistologists.

In 1870, Apathy was appointed to the chair of Zoology at the University of Kolozsvar. He was 27 years old. A few years later he was also in charge of the chairs of histology and embryology (see the biography by A. Abraham, 1963). Kolozsvar is the Hungarian name of the former capital of Transylvania, an old Hungarian settlement which, mostly in the 13th century, received German settlers

and was named Klausenberg. It became part of the Austrian empire in 1691, and was claimed and occupied by Hungary in 1848. As Albrecht Bethe remembers in his obituary of Stephan von Apathy, who died in 1922, von Apathy returned unopened any letter addressed to him at "Klausenburg." His Hungarian nationalism was so strong that he refused to travel through Austria, an attitude which made it a matter of some complexity to reach the Zoological Station at Naples. Stimulated by the example of Anton Dohrn's accomplishments at Naples, Apathy instituted a "table system" at his institute and provided foreign scientists with laboratory space where they could carry out histological studies and get acquainted with his widely acclaimed techniques. Among his guests were Albrecht Bethe, Wilhelm Waldeyer, and a Dutch histologist, J. Boeke, who later became a famous neurohistologist and extended Apathy's studies to the mammalian autonomic nervous system. Boeke remained critical of the neuron theory and maintained that autonomic nerve fibers terminated in a terminal reticulum composed of (neuro)fibrils. Typical of his point of view is his paper of 1949 "The sympathetic end formation, its synaptology, the interstitial cells, the periterminal network, and its bearing on the neuron theory" (*Acta Anatomica* **8**: 18–61). Like Anton Dohrn, Apathy traveled widely to many European universities and became personally acquainted with the best scientists of his day. He put his whole effort into establishing a new "Zoological Station" at Koloszvar, and in 1909 his new Zoological Institute, one of the finest in all of Europe, was opened—complete with loggias and extensive facilities for the maintenance of freshwater and marine animals. As in Naples, the public facilities (the aquaria, museum, lecture rooms), were on the lower floor, the two upper floors contained the research laboratories, the administration, and the library.

How Apathy would have liked to show off his accomplishment to his friend Dohrn! Fate decided otherwise: on 3 October 1909, Apathy attended the funeral service for Anton Dohrn at Jena.

With the end of the first world war, the golden era of Apathy's institute and of his scientific career came to a sudden end. Apathy had become a politician but could not prevent the take-over of Transylvania by Rumania. When he was released from prison, he accepted a position at the Hungarian University at Szeged and tried once again to create a new zoological institute. He no longer had the strength; he died two years later.

J. C. Alexandrowicz: Stretch Receptor Neurons

Stephen von Apathy had survived Anton Dohrn by eleven years. In the meantime, the directorship of the Zoological Station at Naples had been transferred to Anton Dohrn's son Reinhard Dohrn, who, except for his years of exile during 1915–1924, conducted the affairs of the Zoological Station at Naples, guiding this prestigious and precious institution through the political turmoils of a nationalistic era and the so-difficult war and post-war years until he relinquished his leadership to his son Pietro Dohrn in 1954. (The accomplishments of Pietro Dohrn and the later history of the Zoological Station have been critically reviewed in leading articles in *Science,* 1969, and in *Nature,* 1983).

Reinhard Dohrn's diplomatic activities succeeded in 1924 to reach an agreement with Polish authorities to establish a Polish research table at the Stazione Zoologica. One of the faithful scientists using this table was J. C. Alexandrowicz, professor of ophthalmology, and from 1937 Undersecretary of State in the Polish Ministry of Education. Alexandrowicz's meticulous neuro-anatomical studies of crustaceans and cephalopods using methylene-blue staining techniques have earned him a sepcial

place in neurobiology. Perhaps his most important discovery, rivaled only by J. Z. Young's discovery of the giant axons of squid, are the stretch receptor organs of crustaceans. Although this discovery was made at Naples just before the second world war, it became known to the scientific world only several years after the end of the war: when the war started, Alexandrowicz became an officer of the Polish military medical corps. After the defeat of Poland when this country was divided up between Germany and the Soviet Union, Alexandrowicz was taken prisoner by the Russian army, and then was sent with the Polish expeditionary force, known as the Anders Army, to North Africa to help the British defeat the Germans. The contingent, in which he served as education officer, never saw action. When the war ended, Alexandrowicz was taken to England to become a farm laborer. It was Reinhard Dohrn who traced him with the aid of the Red Cross, and, through his connections with members of the Royal Society, initiated the establishment of a special professorship for Alexandrowicz at the Marine Laboratory at Plymouth. Alexandrowicz had lost all his valuable preparations. He now repeated his investigations and in 1952 began his series of publications on the structure and histology of crustacean stretch receptors that have become classics.

Alexandrowicz's investigations are the basis of important physiological work that was begun almost immediately after their publication and led to those discoveries (*e.g.*, Kuffler and Eyzaguirre, 1955) that have become the key to our understanding of how sensory neurons translate a stimulus into a series of nerve impulses, how they encode stimulus strength into an impulse frequency. Alexandrowicz described an efferent innervation of the stretch receptor neurons which was shown later to be purely inhibitory (Eyzaguirre and Kuffler, 1955). The crustacean stretch receptor preparation thus became an important tool in the investigation of inhibitory synaptic transmission. It was in these stretch receptor neurons that the first evidence was obtained that γ-aminobutyric acid (GABA) is the transmitter substance of inhibitory neurons, and that the transmitter action can be blocked by picrotoxin (Florey, 1953; Bazemore *et al.*, 1957). Indeed, it can be said without exaggeration that the stretch receptor neurons discovered by Alexandrowicz at the Zoological Station at Naples have been a cornerstone in the development of neurophysiology. To mention only two of the key findings: it was on stretch receptor preparations that the Japanese physiologist K. Uchizono showed for the first time that inhibitory nerve terminals are characterized by clear oval synaptic vesicles—in contrast to cholinergic terminals which always contain clear round vesicles. The work of the Swedish physiologist D. Ottoson on isolated stretch receptor neurons provided the first clear proof that the site of initiation of the nerve impulse is not the soma of the nerve cell, but the initial segment of its axon.

Ernst Scharer: Neurosecretion

The Zoological Station has been instrumental in yet another important advance in the field of neurobiology: the discovery of what has become known as "neurosecretion," the elaboration and secretion of hormones by nerve cells. In 1928 Ernst Scharrer, then *Assistent* under Karl von Frisch at the Zoological Institute of the University of Munich, was granted the use of a research table at the Zoological Station at Naples. As he stated in a letter to Reinhard Dohrn, he wanted to fix the brain of many species of fish, and "if possible to investigate, with the aid of methylene blue staining, the innervation of the epiphysis." He discovered that certain neurons in the midbrain show evidence of secretion, confirming earlier findings of Carl Speidel (1919). With material from Naples, Scharrer continued his

studies on these "neuroglandular" cells of fishes and extended these studies to higher vertebrates where the same cell type was found. After he had married another pupil of von Frisch, Berta Scharrer, the inseparable couple continued to explore the comparative aspects of "neurosecretion," as the phenomenon was soon to be called: Berta Scharrer in invertebrates, Ernst Scharrer in vertebrates. Their association with Reinhard Dohrn and the Zoological Station became important not only for the development of this important field of neurobiology; the political situation in Germany made life intolerable for the Scharrers, and it was Reinhard Dohrn who helped with their emigration to the United States.

Already before the end of the second world war, in 1944, American scientists like R. E. Cooker (Chapel Hill), A. R. Moore (Oregon), and Ernst Scharrer, urged the president of the National Research Council (the precursor of the National Science Foundation) and Italian authorities to reopen the Statione Zoologica and to support the directorship of Reinhard Dohrn. Thanks to the untiring effort of Ernst Scharrer, who had moved from Ohio to the Department of Anatomy at Denver/Colordao, the National Research Council, as well as Columbia University (Wilson Fund), the American Association for University Women, and the American Society of Zoologists were persuaded to contribute funds in support of the Naples Zoological Station. In the summer of 1946, the president of the National Research Council, Ross Granville Harrison (whose activities at Woods Hole are discussed in other contributions of this Symposium) set up a Committee, chaired by Ernst Scharrer, to aid the Zoological Station at Naples. The Committee, which included as its members E. G. Conklin, Mrs. E. B. Harvey, R. G. Harrison, S. Hecht, L. H. Kleinholz, A. R. Moore, and H. H. Plough, met for the first time on 14 August 1946 at Woods Hole to decide on a program-in-aid to assist in the re-establishment of the Zoological Station at Naples as an international center of biological research. The program envisioned the establishment of additional American research tables, a fund-drive to improve and enlarge the library, and a shipment of food for the Mensa. Further plans concerned the modernization of the laboratory facilities and research equipment. The activities of this committee led to contributions by the Rockefeller Foundations and the UNESCO. The committee advised the Zoological Station in matters of library acquisitions and the purchase of research equipment. After 1950 the newly established National Science Foundation, the Lilly Endowment, Inc., and the Rockefeller Foundation increased the American engagement in the affairs of the Zoological Station enormously—but this is not the place to record the international ramifications of the Zoological Station and the history of the material support it has received from the international scientific community (which, after all, includes members of other nations that have made substantial contributions to the development of the Zoological Station). We return, therefore, to the topic of the role of the Zoological Station at Naples in the development of neurobiology.

On the initiative of Ernst Scharrer and Wolfgang Bargmann, the Zoological Station hosted, in 1953, the first International Symposium on Neurosecretion (this was the fourth international symposium held at the Zoological Station). This event has a special place in the history of biology because it was this symposium that established the concept that neurons produce hormones and that neurosecretion is an essential feature of the chemical control of animal development and function.

J. Z. Young: Giant Axons, Learning and Memory

It is impossible to review the relationship between the Zoological Station and the neuron without mentioning the research on the giant axons of squid, discovered

by J. Z. Young in 1936 when he worked at this institution. Since Prof. Young will review the history of this discovery in his lecture, it will be sufficient to restrict the discussion here to some further development of research made possible by the incredibly large size of the "giant synapses" between second- and third-order giant axons. In 1966 Berhard Katz and Riccardo Miledi from the University College in London came to the Stazione Zoologica to investigate the relationship between calcium and transmitter release. Their experiments have become classics; they prove that extracellular calcium is essential for transmitter release to occur and that calcium ions enter the nerve terminal when this becomes depolarized by the incoming presynaptic action potential.

The year-round availability of *Octopus* at Naples, and the recognition of the advanced development of the brain of these animals has prompted Y. Z. Young to embark, at the Statione Zoologica, on a study of learning and memory in these creatures. This was made possible by a large grant to the Stazione Zoologica for the establishment of a large "cephalopod facility" which, in its best days, included more than two hundred tanks in which as many octopuses could be individually housed and maintained. Together with several collaborators, especially Bryan Boycott, Martin Wells, and John Messenger, he mapped the neuronal circuits of the octopus brain and through ingenious training experiments he explored the learning ability of these animals. These studies led to new concepts of the neuronal mechanisms underlying memory. Several important monographs resulted from this research: M. J. Wells: *Brain and Behaviour in Cephalopods,* 1962; J. Z. Young: *A Model of the Brain,* 1964; J. Z. Young: *The Anatomy of the Nervous System of* Octopus vulgaris, 1971; and J. Y. Young: *Programs of the Brain,* 1978.

Conclusion

By providing research facilities near the sea where marine animals can be readily obtained and maintained, and, more importantly perhaps, by providing the intellectual atmosphere conducive to intensive research and stimulating interaction with other scientists, the Stazione Zoologica has permitted major advances in neurobiology to occur. As long as this institution was able to pursue the goals envisioned by its founder, Anton Dohrn, it was eminently successful. But such simple words cannot explain the impact the Zoological Station at Naples had on biologists all over the world. Intentionally I use the word 'biologists' and not the abstract form 'biology.' The Stazione Zoologica has been dominated by the spirit of its former directors, by the immense human dimension of its founder Anton Dohrn, by that great European, Reinhard Dohrn . . . all this has been attested to by so many public statements, that no further emphasis is needed. The most recent eulogies were presented (typically, in four languages) by dignitaries from many countries on the occasion of the celebration of the 100th birthday of Reinhard Dohrn on 13 March 1980 in the Vila Pignatelli in Naples (*Reinhard Dohrn 1880–1962,* edited by C. Groeben, 1983).

And yet, neither the location nor the personalities of the directors can explain the miracle of the "Naples experience" (to quote Maurice Wilkins) or the affection all those great scientists felt, and still feel, for the Zoological Station. Good research institutes can be found in many places in many countries, and the Statione Zoologica is certainly not among the best equipped laboratories—perhaps it never was! Nor has it been attractive because it harbored a local scientific genius at whose feet it was desirable to sit, in whose laboratory it was essential to learn methods unattainable anywhere else. The idea of an international home for an international science, nay, for the unfettered pursuit of the highest ideal of science, this original idea of Anton

Dohrn was so infectious, that, from the start, it caught the imagination of all those great minds who came in contact with it: Charles Darwin, Thomas Henry Huxley, Thomas Hunt Morgan, Edward Beecher Wilson, Hermann von Helmholtz, Emil Du-Bois Reymond, Filippo Botazzi, Silvestro Baglioni—and Fridjof Nansen, Stephan von Apathy, Albrecht Bethe, J. C. Alexandrowicz, Ernst Scharrer, J. Z. Young, but also of Benedetto Croce, Theodor Heuss, . . . the list is endless.

The Zoological Station became a place of the mind, an ideal jointly possessed and cherished by all those who experienced it. This is the reason why the organism of the Zoological Station was able to survive: not because it was itself strong enough to surmount all the adversities it encountered in its long history, but because it was revived from the outside on the strength of the idea carried by the community of all those who kept this idea alive and found ways to revitalize it both spiritually and materially. Science is not an abstraction but an immensely human activity. It is lived, not written, thus it needs a true home, not only a laboratory or an office. The Zoological Station at Naples has been such a home and has been, and is being regarded with that special kind of nostalgia accorded only to those special places in which the true spirit of man is recognized. Thomas Hunt Morgan called it a "holy city." Our present age would do well to live up to its tradition.

The brief histories given here are the stories of important scientists and of their important discoveries. But they are also memorials of great ideals, passions, and sacrifices, and they bear witness to the importance of a great dream which happened to come to life at Naples in the Zoological Station, the creation of that remarkable man, Anton Dohrn.

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Important sources were the *Geschichte der Mikroskopie* edited by H. Freund and A. Berg (vols. 1 and 2, 1963, 1964), Alfred Kühn's important work *Anton Dohrn und die Zoologie seiner Zeit* (1950), Theodor Heuss' biography of Anton Dohrn (2nd edition, 1962), and the Festschrift *Reinhard Dohrn 1880–1962* edited by Christiane Groeben in collaboration with Antonie and Pietro Dohrn (1983).

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CEPHALOPODS AND NEUROSCIENCE

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Introduction

Study of cephalopods at marine laboratories has provided material for some of the outstanding discoveries of neuroscience in this century. The giant nerve fibers are the most conspicuous example, but studies of photoreceptors and the memory mechanisms of the brain have been very fruitful, as has work on chromatophores and many other topics. It would be impossible to summarize all this work but it may be interesting to show the sequence in which some of it has developed at Naples, Plymouth, and Woods Hole, in much of which I have been concerned.

Eyes

Perhaps the earliest contribution of cephalopods to fundamental neural processes was the discovery of the electroretinogram by Fröhlich at Naples in 1914. The curious electrical phenomena in the rhabdomes are still only partly understood and have been the subject of many later investigations. Outstanding has been the demonstration by Hagins and McGaughty (see Messenger, 1981) that the opening of channels to produce generator potentials takes place locally, near the site of photon absorbtion in a rhabdome. Speaking of the retinal pigments will remind us of the use made by Hubbard and Wald at Woods Hole of cephalopod eyes to provide the rhadopsin for their fundamental research. Indeed the history of the use of these eyes for neuroscience merits a symposium of its own. Cephalopods appear to have no color vision, in spite of their own colorful displays (Messenger, 1981). But the capacity to detect the plane of reflected polarized light, first suggested by the geometry of the rhabdomes (Young, 1960; Saibil, 1982) and proved experimentally at Naples by Moody and Parris (1961) and by electrical recordings, may provide a sort of substitute for color vision (Saidel *et al.,* 1983).

Statocysts

The statocyst is an organ, one of whose major functions is stabilization of the visual image. It has been investigated at Naples by Young (1960) and Wells (1960). Thorough studies have been made by Budelmann at Regensburg using large numbers of octopuses and cuttlefishes carried alive from Naples. He and I have analyzed the oculomotor control system (Budelmann and Young, 1985). Recently he has discovered that an octopus monitors its fast and slow movements separately by a unique system of large and small cupulae (Budelmann and Williamson, 1985).

Another recent development has been the discovery that the peduncle lobe and basal lobes of the brain contain systems of small cells with parallel fibers. These resemble the vertebrate cerebellum and like that organ are involved in the optomotor reflexes.

Measurement of the statocysts of many species collected from Plymouth, Naples, Woods Hole, Miami, and Hawaii have shown a system similar to the semicircular canals of vertebrates (Stephens and Young, 1975; Maddock and Young, 1984). The

canals are formed by a series of knobs, the anticristse. They are best developed in the rapidly moving loliginids and ommastrephids. In the slowly moving neutrally buoyant forms, the statocyst is large and empty.

Extraocular Photoreceptors

What may be called the modern epoque of cephalopod research at Naples was begun by Enrico Sereni who made many experiments on the chromatophores and salivary secretion, summarized in a long article in 1930. At the time of his early death he and I were collaborating in a study of regeneration of the stellar nerves, which was completed after his death (Sereni and Young, 1932). In the course of this study I was attracted to a small orange spot at the hind end of the stellate ganglion of *Eledone*. I cut sections of it, with no hypothesis other than curiosity. It proved to be a hollow vesicle into which passed a number of projections, apparently of nerve cells. After discussion with Sereni it was named the epistellar body (Young, 1929). I was interested at the time in the vertebrate adrenals and made the hypothesis that these projections into the epistellar cavity were secretory. Ernst Scharrer eagerly seized upon this as one of the earliest examples of neurosecretion. But he and I were sadly mistaken. Forty years later Howard Bern, himself an endocrinologist, thought it time to study this organ properly. The E.M. quickly showed that the processes inside the epistellar body are *rhabdomes* (Nishioka *et al.*, 1966). It is not a gland at all but a photoreceptor, though without any lens or other dioptric apparatus. Alex Mauro working at Naples and Ischia confirmed that it produces its own minielectroretinogram (Mauro and Baumann, 1968). What can this photoreceptor be doing *inside* the mantle? The epistellar body is especially large in deep-sea octopods, which are transparent. One hypothesis is that it serves to detect the presence of a mass of luminous material in the mantle, which would attract a predator. The oesophagus is deeply pigmented, presumably for the same reason. However Houck (1982), working at Hawaii, has recently shown that in octopuses with the optic nerves cut diurnal rhythms can still be entrained by light, perhaps detected by the epistellar bodies.

The extra-ocular photoreceptors in decapods are in the head, not on the stellate ganglion (Thore, 1939; Boycott and Young, 1956). They have been thoroughly studied by R. E. Young (1978) at Hawaii in many species of squid. In some mesopelagic forms such as *Abraliopsis* they serve to monitor the downward illumination emitted by photophores for countershading. For this light to be effective in making the squid invisible from below it must match the downwelling light. This match is ensured by the photosensitive vesicles which are in two sets, one looking up to the surface and the other towards the animal's own luminous organs (Young and Roper, 1976). The system even ensures an appropriate match to the wave length, if necessary, in moonlight!

The extra-ocular photoreceptors are even larger in the bathypelagic squids, such as the cranchiids, many of which proceed to depths beyond the range of daylight, especially for reproduction. Here the photoreceptors must have another function. I suggest that they monitor the depth at which to spawn. They provide huge irregular masses of photosensitive material and their nerves connect with the peduncle lobe of the brain, which is probably concerned with movement in the vertical plane. It may be that the squids continue to proceed deeper and deeper until no photons are captured even by these large masses of pigment. When the light goes out it is dark enough to breed! Conversely the photoreceptors prevent rising into the dangerous lighted zone.

Giant Fibers

These discoveries are all exciting but even greater developments have flowed from my original curiosity about the epistellar body. Having found it in octopods I naturally also made sections of the stellate ganglion of decapods. No epistellar body was there but instead I found the giant nerve fibers. I am often asked at what date this discovery was made but can give no clear answer. Sections of the ganglia of *Loligo* were made at Naples in 1929 but at first I thought these large spaces were veins. The axoplasm does indeed look quite like blood in some sections. Then I followed them towards the hind end of the ganglion where, as we now know, they originate by the fusion of the axons of many cells. This seemed to me, as a faithful Oxford follower of Sherrington, to be so unlikely that it took some years to persuade myself of it. However in the collection there is a slide, labeled in my handwriting "1 · 5 · 30," which is a thick section clearly showing the axons dividing and passing to many cells of the giant fiber lobe. So I must have "known" their anatomy at that date, but was not sure enough to publish.

During the early 1930s I worked at Plymouth, mostly with *Sepia,* where the giant fibers are smaller and there is no giant fiber lobe. The first publication was therefore a note in the *Journal of Physiology* in 1934 claiming that the axoplasm is fluid, which we now know to be an error. Then in 1936 there was a fuller account suggesting that the epistellar body had been derived from the giant fiber lobe of an ancestor, which is probably another error.

However by now I was fully convinced that they were nerve fibers, and in 1936 was able to prove this by simple experiments at Woods Hole (Young, 1938). Several others then joined me: Bronk, Gerard, and Hartline all tried to show action potentials but the primitive oscilloscopes of those days worked poorly and my distinguished colleagues could not show reliable action potentials by electrical stimulation. One day Keffer Hartline and I hooked a fiber to an amplifier and speaker and put a crystal of oxalate on the end; out came a wonderful buzz—the first giant fiber impulses.

K. C. Cole and Curtis were soon studying the electrical properties of the membrane and Frank Schmitt and Richard Bear showed me how to study biophysical structure properly (Bear *et al.,* 1939). Material collected that summer at Woods Hole provided the basis for a full study of the giant fiber system of *Loligo* (Young, 1939). It was only at this time that I discovered that the first order giant cells in the brain had been illustrated by Williams (1909). His excellent monograph was published in Holland and so far as I can discover the giant fiber system was never mentioned throughout the succeeding years. Williams followed the large fibers into the stellate ganglion and stellar nerves but he seems to have supposed that they ran through the ganglion without synapse. He gave no figure of them.

The next phase of work on the giant fibers was mainly at Plymouth. Pumphrey and I showed (1938) that the conduction velocity follows the square root of the diameter. Rapid conduction by giant fibers is an expensive luxury for a species. In these experiments we were helped by Alan Hodgkin, then a student at Cambridge; this was the first introduction of the Cambridge team to the squid fibers.

The axons provided the material for the first direct measurements of the internal potassium concentration of protoplasm, made independently by Bear et al. (1939) and Webb and Young (1940).

The full development of the potentialities of the giant fibers occurred after the war and I shall not try to follow the details. Outstanding achievements were the placing of an internal electrode and the emptying and refilling of the axon by

Hodgkin and Huxley. These investigations provided the data that enabled them to deduce the equations of the ionic exchanges that are involved (Hodgkin and Huxley, 1952).

The special usefulness of the fibers is that they allow monitoring by electrodes on both sides of the membrane. Numerous workers have used this property for studies of membrane transport at Woods Hole, Plymouth, and Naples, continuing to the present day at Plymouth with the work of Keynes and Baker and Haydon, to mention only three out of many. Miledi and Katz and other groups have been able to study the two sides of the synapse at Naples. The masses of axoplasm and sheets of membrane have provided opportunities for the work of thousands of physiologists, biochemists, and biophysicists and will continue to do so in the future. As new problems and techniques appear these fibers will provide the material of choice for testing them. It is curious to think how different neuroscience would have been had I not made sections of a yellow spot—*out of simple curiosity.* It is easy to say that the fibers would have been discovered by someone else soon. But would they in the present climate? Who would write a grant application to study the possible structure of an unknown organ? It is an example of the need to allow people to pursue whatever curious subject may interest them.

Memory

The sections of the brains of squids and cuttlefishes that were made to study the giant fibers showed me many other wonderful things. The supraoesophageal lobes include a dozen distinct lobules, each with a different pattern of cells and neuropil. Surely these would provide a good opportunity to study higher nervous activities, such as memory. I felt that this was an opening even more important than was offered by the nerve fibers. Already in the 1930s there was a moderately good idea of how nerve impulses are conducted. Hodgkin and Huxley were able to carry this much further and the giant synapse provided great opportunities. But the really mysterious problems of neuroscience were hidden there in the neuropils of the higher centers. Biophysics was not ready to attack them, and still cannot do so even in 1984.

However it seemed to me that a start should be made, and Sanders and I were able to show at Plymouth that the learning power of *Sepia* is indeed dependent on the vertical lobe (1940). After a long interval in the war, while studying nerve regeneration in mammals and men, I returned to the problem of memory at Naples. *Octopus* provides even better opportunities than *Sepia* and proved to be a splendid learner. The supply at Naples seems to be inexhaustable. The Posillipo fishermen have been able to bring in 20 or more octopuses a day in excellent condition and the Stazione has generously provided space for special tanks to be built with funds from the British Science Research Council. These facilities are still available.

With the cooperation of Boycott, Wells, Sutherland, and many others, the two memory systems of the octopus, visual and tactile, have been thoroughly explored (see Wells, 1966; Young, 1983). Lesions have shown that various lobes are involved in learning, each in a different way. The visual and tactile memory systems each includes four lobes with distinctive structure and function. Unfortunately for some reason it is difficult to record the electrical activities of octopus neurons. The afferent fibers proceeding from the retina and statocyst have been thoroughly investigated, but little is known about activities within the brain. There have been many investigations of the transmitters involved since the classical demonstration by Bacq (1937) of the huge amounts of acetylcholine in the optic lobes. Among

many others Juorio (1971), Juorio and Barlow (1976), and Tansey (1979) have shown the distribution of amines in the brain, mostly using material obtained at Naples.

Studies of cephalopods have not revealed all the secrets of the mechanism of learning but they have shown much, and may show more. It may be claimed that we already know from work with large-celled gastropods, such as that of Kandel, that memory involves changes in synaptic conduction. This is a great advance but does not tell us how representations stored in the brain enable an animal or man to recognize a rectangle. There are properties of *aggregates* of neurons and we still require brains such as those of octopuses that are suitable for studies of them. It will need special methods that cannot yet be seen, and I doubt whether multiple electrodes will serve. Some methods must be devised that can show how numerous neurons interact. The various neuropils of an octopus may provide the material that is needed, just as the giant fibers of the squid will allow testing of new methods for the study of membranes.

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NICKED BY OCCAM'S RAZOR: UNITARIANISM IN THE INVESTIGATION OF SYNAPTIC TRANSMISSION

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Introduction

Before the modes of synaptic transmission were well enough understood to decide the matter, chemical and electrical mediation were widely accepted as the two possibilities. Neurophysiologists in general thought that transmission was electrical, because axonal conduction was electrical and they saw no need for an additional mechanism. Furthermore chemical transmission seemed too slow. On the other side, pharmacologists favored chemical transmission, because they worked with drugs and had a great deal of evidence for chemical sensitivity (and some for chemical transmission) at peripheral sites including viscera and skeletal muscle.

The motif of this article comes from a story Harry Grundfest used to tell. In his 1947 paper in *Annual Review of Physiology* he inclined toward the view that interneuronal transmission is electrically mediated, as is axonal conduction, and in his letter of submission with the manuscript, he said that in spite of evidence for chemical transmission he remained an enlightened unitarian. By the time of his 1957 review he, and others, were convinced that synaptic transmission was chemically mediated. He recalled the comment written on the end of the manuscript by an editor who remembered the earlier letter: "Enlightened unitarianism grows dim."

Although chemical transmission was established and unity of synaptic transmission and axonal conduction defeated, unitarianism lived and still does. Occam's razor, the mode of inference in which the simplest explanation is favored, remains in use. I shall give several illustrations from the controversy over synaptic transmission of Occam's razor cutting both ways, instances where the simplest explanation was incorrect or incomplete, and the investigator was misled by his preference for a unitarian view. Biological reality does have many unifying principles, but life is complicated and also historical. Nervous systems in their evolution have come to use many different mechanisms.

Both electrical and chemical transmission were proposed for the neuromuscular junction in the 1800s (*cf.*, Brazier, 1959). In 1904 Elliot observed the similarity between the actions of sympathetic nerves and adrenalin. Recognizing the homology between adrenal glands and sympathetic ganglia, he suggested that the nerves acted by releasing adrenalin. This proposal was made in a proceedings note in the *Journal of Physiology*, but for reasons unknown to me he failed to mention the idea again in the detailed publication of the data appearing the following year (Elliot, 1905).

Loewi is commonly given credit for establishing chemical transmission with his 1921 experiment on the Vagusstoff. Indeed, of the two essential criteria for identifying a transmitter, evoked release of the putative transmitter and identity of action of the transmitter and the neurally released material, Loewi's experiment was the first to demonstrate release. In his 1933 Harvey Lecture Loewi wrote "In the year 1921 I was able to prove without doubt the correctness of the fundamental idea" that sympathetic and parasympathetic nerves liberate a chemical substance that produces the postsynaptic action. But he did not overgeneralize. He raised the

possibility of chemical transmission in the central nervous system, seeing that it would provide a nice mechanism for temporal summation, but noted (p. 228) "the experimental proof may be rather difficult to obtain." He continues (p. 232)

> A priori one can imagine that in cases where the effect of stimulation takes place in an almost immeasurable space of time and ceases practically instantly after the stimulus is over, as for instance in the case of nervous stimulation of striated muscle, there is hardly enough time for a substance to be formed and nearly simultaneously rendered ineffective. But the time factor is not a decisive proof for or against a humoral mechanism in the case of spinal nerves. Personally I do not believe in a humoral mechanism existing in the case of striated muscle.

Although Loewi's work was important in establishing the possibility of chemical transmission, comparable experiments were done for electrical transmission much earlier by Matteuci, who showed that the electricity produced by a contracting muscle would stimulate a nerve (see Brazier, 1959). A nerve generates electricity, but one can question whether it is in the right amount, at the right time and in the right place to account for synaptic transmission. The same question applies to Loewi's experiments. Occam's razor suggested that the neurally released transmitter with the same action as caused by nerve stimulation was indeed released appropriately in terms of amount, time, and place, but a definitive demonstration of all these properties has still not been made, at least at any synapse where transmission is rapid. Other electrophysiological criteria turned out to provide the evidence that ultimately convinced the doubting electrophysiologists (such as Grundfest). And in my view it was Occam's razor, correctly used, that convinced the pharmacologists before all the data were in.*

J. C. Eccles and Enlightenment

Eccles figured prominently in what was often termed the sparks and soup controversy, and his history of the subject is insightful as well as first hand (Eccles, 1982). He was convinced of chemical transmission in respect to sympathetic innervation prior to the second world war. By 1948 he also found Kuffler's experiments in 1942 and those of himself and collaborators to be a valid demonstration of chemical transmission at the (frog) neuromuscular junction. The prolongation of the PSP by eserine without change in the brief nerve response was indeed highly suggestive. But in the absence of really knowing the anatomy and the transmembrane potentials, one can still regard the case as somewhat open. Indeed in a 1948 review of most of these experiments Kuffler writes a rather ambiguously worded passage indicating uncertainty, although it could be construed as implying chemical. He really did mean uncertainty for his note added in proof cites an Eccles review (1948) stating that chemical transmission was definitely established. It is interesting that Kuffler's work is frequently referred to in that Eccles review. Although the section discussing neuromuscular transmission is unclear as to mode, a direct statement is found on p. 112 "the electrical theory of transmission provides a satisfactory answer for the spinal cord, which contrasts with the neuromuscular junction where transmission appears to be exclusively cholinergic." Also on p. 107 "In every respect the observations of Bullock on the squid giant synapse conform

* Ernst Florey in the discussion of the oral presentation of this paper told of a visit to Loewi in New York after World War II. Loewi reported to Florey that he had recently had an unpleasant experience while attending a Rubinstein concert. He was so distracted by the evident impossibility of such rapid and complex motor acts being mediated chemically that he could not enjoy the music.

with the predictions of the electrical theory," observations that electrophysiologically were very similar to those at the neuromuscular junction. Chemical transmission in muscle was accepted, but electrical transmission between neurons was being conserved.

In respect to Eccles and Kuffler on the neuromuscular junction, I recall Paul Cranefield referring to a paper where the coauthors disagreed strongly about the significance of their findings. In writing the discussion they finally compromised on the wording "one of the authors is forced to conclude that . . ." The investigation of synaptic transmission produced many inferences about whose compelling nature there were strong differences of opinion. Intracellular recording clarified the situation greatly.

Eccles and co-workers in their landmark paper (Brock *et al.*, 1952) (justifiably) stated that their data established chemical transmission for neuronal inhibition. The demonstration did not involve identification of the transmitter or measurement of its action and release, but rather intracellular recording of activity that could not (reasonably) be mediated electrically. They were suitably careful about excitatory transmission and only said that it was probably chemically mediated. Fatt and Katz (1951) had already applied intercellular recording to the neuromuscular junction, and characterized chemically mediated excitation to an extent that had not been possible previously. They were also studying transmission in a crustacean muscle where inhibition resulted from a conductance increase that could not be electrically transmitted from the presynaptic fiber (Fatt and Katz, 1953). Of course this was at a crustacean neuromuscular junction not known to be a model for mammalian CNS. Fatt subsequently joined Eccles for a collaboration in which the electrophysiological insights of Fatt and Katz were applied to both excitatory and inhibitory synapses in the cat spinal cord. Eccles, in '57, wrote: "It can now be taken as established that transmission across synapses occurs not by the spread of electrical currents, but by the specific chemical substances which impulses cause to be liberated from the presynaptic membranes" (p. 67).

Eccles conversion was an impressive mental feat in that he was able to let go rapidly of an idea he had strongly fought for. To be sure, the influence of Karl Popper had led him to push the idea of electrical transmission perhaps harder than justified until it was finally falsified (for cat motoneurons). The pendulum swung in terms of the body scientific as well, and my impression is that at this time almost everyone believed that synaptic transmission was chemically mediated. However, Furshpan and Potter (1959) were studying the crayfish giant motor synapse. Wiersma had previously shown that it transmitted impulses in only one direction and from sensitivity to block by pharmacological agents he inferred transmission to be chemically mediated. It was an attractive synapse because both pre- and postsynaptic axons were large enough that it appeared (and was) possible to penetrate both elements close to the synapse. Furshpan and Potter found that here transmission was, after all, electrical, and unidirectional transmission of impulses was due to rectification by the membranes in the synaptic region which were known to be closely apposed. Eccles easily accepted these new findings and in his 1961 review had a section on electrical transmission. He also proposed that the junctions between segments of septate axons found widely in annelids and arthropods "should not be considered synapses" because they conduct in both directions, but if they were considered synapses "they would be examples of "the simplest type" of electrical synapse" (p. 363).

Only later did he come to accept the septal junctions as synapses which are, by his definition, close appositions "specialized for the transmission of excitation or

inhibition" (Eccles, 1964 p. VI). [For the record, Watanabe (1958) independently discovered electrical coupling between cardiac ganglion cells in an arthropod, although in the absence of morphological data (still absent in many instances in arthropods including this one) he thought the cells were syncytial.] Perhaps because electric transmission was initially found in invertebrates Eccles (1961, p. 366) was led to write

> It seems probable that many examples of electrical [sic] transmitting synapse may be discovered when invertebrate nervous systems are intensively investigated. With the vertebrate nervous system the invariable presence of a considerable synaptic delay would exclude electrical transmission as significantly contributing to any of the synaptic transmissions that have been investigated by intracellular recording.

For the record, there are many instances in mammals and lower forms where synaptic delays at chemical and electrical synapses are difficult to distinguish (*cf.*, Bennett, 1977).

At a meeting on the thalamus in 1965, I presented a paper on how electrical synapses synchronized neural firing in fishes and suggested these systems as a possible model of mammalian CNS synchronization (Bennett, 1966). Afterwards Eccles was heard to say in effect that it was all very well for fishes but Bennett would never find electrical transmission in mammals (D. P. Purpura, pers. comm.). I admit that my presence at the meeting was more a result of my being in the institution of the organizers than of their conviction that the fishes' physiology was pertinent to the mammalian thalamus.

Others did go on to find electrical transmission in the mammal (reviewed in Bennett, 1977, and Korn and Faber, 1979, and new examples continue to be discovered). Eccles still writes somewhat perjoratively in 1982 that electrical synapses "are relatively rare in the mammalian brain and it has yet to be shown that they are functionally important in the brain" (p. 337). For the mammalian brain he prefers there to be only a single important mode of transmission. I have often argued that there are many synapses where it is difficult to see a relative advantage of excitatory chemical over electrical transmission (*e.g.*, Bennett, 1977), but in this area of course I am not disinterested and my arguments can be seen as serving to increase the importance of my own research. Nevertheless, in the absence of experimental data it is difficult to conclude that a distinct group of synapses are unimportant in the operation of the central nervous system.

H. Grundfest and Neo-Unitarianism

Let us now return to the 1950's and Harry Grundfest's 1957 review. Grundfest proposed that subsynaptic membrane was electrically inexcitable and that this property was essential in its operation, and thus all synaptic transmission was chemical. (I came to work in Harry's lab at this time, shortly after finishing graduate school.) The originality of the proposal of electrical inexcitability is arguable and Fatt and Katz had previously stated that ACh action at the neuromuscular junction is unlike that of an electric field which causes generation of an action potential. Eccles (1957, p. 52) wrote independently that by "analogy with the subsynaptic membrane of the neuromuscular junction [and other examples] . . . it is possible that the subsynaptic areas [of motoneurons] are incapable of responding by impulses." Grundfest did bring a large amount of data together and in my view his major contribution in this regard was in emphasizing the importance of a general physiology that included all synapses and not just the favored few.

Given that Grundfest had adopted electrical inexcitability and chemical transmission as universals, a grand generalization, he was presented with a problem when electrical transmission was definitively established. He (with Kao) wrote in 1957 "The term synapse assumes more meaning than merely the physical apposition of two adjacent excitable cells. Synaptic transmissional excitation must therefore be initiated by a process of specialized, secretory activity at the presynaptic terminals" (p. 569).

It was arguable that a necessary property of a synapse is unidirectional action (as Eccles did briefly) and Kao and Grundfest saw the septa not as synapses, but as "ephapses without synaptic function, demarcating ontogenetic cellular boundaries." The term ephapse was coined by Arvanitaki (1942) to denote artificial junctions made by placing two axons together; she proposed these junctions as a model for (real) synapses. The rectifying electrotonic synapse described by Furshpan and Potter was not so easily excluded because it exhibited polarized or unidirectional conduction. Kao and Grundfest wrote "It remains to be seen whether this 'electrically excitable synapse' is a condition found at other junctions or whether it represents an abandoned evolutionary variant" (p. 570). (One sees more vertebrate chauvinism here. Arthropods represent the peak of another branch of evolution.)

Grundfest's later solution to the problem of electrical synapses was to change the name. In his 1959 chapter, all electrical synapses have become ephapses. Grundfest recognized that the crayfish "junction meets the criteria of anatomical discontinuity and transmissional polarization" (p. 192), (now we know there is cytoplasmic continuity for small molecules) but discusses the junction's profound differences from chemically transmitting synapses with electrically inexcitable subsynaptic membrane.

He also recognized that special geometric properties alone can lead to polarized transmission (at electrical synapses or ephapses, p. 190), but now to him "the crucial distinction is whether current flow in a presynaptic terminal can excite" the postsynaptic element. Since at chemical synapses the presynaptic current is "far too small to excite the postsynaptic cell," the electrical synapses must be something else; he chose ephapses. There is a clearly illogical step here. All synapses are unidirectional; chemical synapses are unidirectional and not electrical. Thus all synapses are chemical and not electrical (this is the mistake), and if one finds a junction that is unidirectional and electrical, it can't be a synapse. I do not believe that this was the way in which Grundfest arrived at the description of electrically transmitting junctions between neurons as ephapses. Rather the constellation of properties which he viewed as integral to synaptic transmission appeared to derive from chemical mediation. If some synapses were electrical, the thesis would have required major revision, and it was simpler to call electrical synapses by a different name.

I leave the question of electrical inexcitability with a few further comments. Many of the properties of chemical transmission that Grundfest cites can arise in other ways, and electrical synapses can exhibit virtually all of them (except PSP reversal). I never found it compelling that subsynaptic membrane should be inexcitable, because it always seemed possible that a transmitter could act on an electrically excitable channel. K ions released by activity depolarize adjacent cells by changing the driving force for both excitable and inexcitable channels, and there are many examples of K release by neurons affecting other neurons. The K effects might be considered ephaptic rather than synaptic (although chemically mediated), but the action can still be excitatory on electrically excitable membrane. Recently many modulatory synapses have been described where transmitters act to alter an

electrically excitable conductance (Tsien and Siegelbaum, 1983). To be sure most of these actions are probably mediated by a second messenger that is intracellular, and the subsynaptic membrane where the transmitter acts is not directly involved in impulse generation.

In current terms we know many channel macromolecules that are affected by transmitters, other chemical agents and electric fields (*cf.* Bennett *et al.*, 1984). It is reasonable that for an intramembrane protein undergoing a conformational change there would be a dipole moment change that would confer some degree of electrical sensitivity. This sensitivity might be greater as in the usual channels involved in impulse generation or lesser as in most transmitter evoked changes at subsynaptic membranes of chemical synapses. But the general prediction is that any chemically evoked change will also exhibit some degree of electrical sensitivity. Furthermore, channels primarily sensitive to potential may also be sensitive to regulatory molecules, pharmacological agents, and toxins. I do subscribe to Grundfest's provocative view that electrical inexcitability as determined electrophysiologically provided the only "direct" evidence for chemical transmission. Many synapses are accepted as chemical on electrophysiological grounds with no knowledge of the transmitter (let alone evoked release and identity of action, *cf.*, Brock *et al.*, 1952). However, one man's direct evidence is another man's tortured reasoning, and chemical transmission would not be nearly so convincingly demonstrated by electrical inexcitability if there were not all those data on transmitter action and transmitter release.

My exposition of where Grundfest went slightly astray should be evaluated in light of my own agenda. While my recollection is that I did not accept Grundfest's constellation of properties at the time, the real difficulty came later when my collaborators and I began to find electrical synapses in modest profusion. It was not in my self interest to be working on a lower class of interneuronal junction, with a connotation of artificiality, regardless of whether they could exhibit most of Grundfest's properties. There was no doubt another factor that I have heard called Feldberg's dictum, that is that a scientist would rather use another scientist's toothbrush than his [or her] terminology.

There were several important precursors to electrical transmission as demonstrated by Furshpan and Potter. As noted above, Kao and Grundfest (1959) saw the septa as providing little hindrance to local circuit, electrical propagation although the septa were described as not synaptic. Bullock in 1945 wrote (p. 70):

> The high speed of conduction and its unpolarized character are significant in view of the apparently synaptic nature of the system as demonstrated histologically. These properties are compatible with the [supposition] that the synapse is not inherently polarized nor delaying but is only so as a result of the particular anatomical relations prevalent in vertebrates and that these properties should not be a part of the definition of the synapse.

The suggestion that septal synapses are like all other synapses is again overinclusive, but the description accurately applies to many electrical synapses in vertebrates as well as invertebrates.

Not everyone took a unitarian view during these developments. Fatt wrote in 1954:

> it is probable that electrical transmission occurs at certain other junctions. One possible arrangement, which may be envisioned to give a high degree of electrical interaction is for two fibers [of about the same dimensions] to be actually touching and for the membrane in contact to have a low electric resistance

> compared with that in neighboring parts of the fiber. The synapse would then serve to direct current between the interior of the two fibers, while active membrane changes would occur in the neighboring regions [p. 204].

Here is an accurate description of transmission at many electrical synapses; many more if one ignores the qualification as to similarity of size of the fibers. As an aside there is an implication of absence of excitability in the connecting membrane. He went on:

> A case in which there can be little doubt that electrical transmission operates is in the nervous system of the crayfish, where successive giant nerve cells, each extending along one segment, . . . form the lateral giant nerve fibers. Transmission takes place in either direction and such chains of nerve cells [form] synapses where transmission occurs electrically [p. 705].

Thus, the stage was thoroughly set for electrical transmission. I find it admirable that in the laboratory that many consider the primary source of chemical transmission, there was recognition that in some cases transmission was very probably electrically mediated. Fatt thought, for reasonable cause, that transmission at the motor giant synapse of crayfish was chemical, but the basic understanding that led to Furshpan's and Potter's important findings were there.

Nachmansohn and Single-minded Unitarianism

David Nachmansohn will be used to provide a brief coda to the longer discussions above. He held with an amazing perseverence to a unified theory of chemical mediation of action potentials, all action potentials everywhere, but believed that synaptic transmission was electrical. His thinking came to be a somewhat distorted mirror image of the majority view.

The cholinergic system was an enduring concern of Nachmansohn, and he made many truly major contributions in respect to the properties of acetylcholine esterase and the discovery of choline acetylase (or choline acetyltransferase) and coenzyme A. Early on he and his collaborators, in studying the electric eel, found that the concentration of AChE per unit length of electric organ was quite linearly related to the voltage developed per unit length. The current hypothesis to explain this finding would be that voltage is proportional to the number of cells in series, and the number of cells per unit length is greater in anterior regions. The AChE is largely found on the innervated face of cells, so the amount of AChE is proportional to the number of cells, hence voltage and AChE are related. At the time of Nachmansohn's finding the series summation in electric organs of essentially ordinary membrane potentials had not been established and the inference of ACh's direct involvement in potential generation was a tenable hypothesis. The Nachmansohn group proceeded to find a great deal more data of a pharmacological kind that supported the involvement of the cholinergeric system. Also, negative evidence such as the failure of polar cholinergic agents to act on ordinary axons was accounted for by postulation of permeability barriers that protected the actual sites of impulse generation. During these developments there were questions raised by others about specificity or reproducibility of some of the results in agreement with the theory. Moreover as data accumulated it became necessary to postulate permeability barriers on the inside as well as outside of the active membrane. The theory, although increasingly ornate, was now extremely difficult to disprove, certainly by Nachmansohn's standards. In the early seventies he elaborated a highly specific version of how ACh was involved in the permeability changes underlying action potential generation. (He did not deny the permeability changes of ion fluxes.)

His view of synaptic transmission was surprising given that he required a chemical step in axonal conduction. In emphasizing the biochemical unity of life, "Nature has shown little imagination in modifying chemical mechanisms associated with given functions" (Nachmansohn and Neumann, 1975), he wanted transmission to be electrical. In 1961 he wrote

> The action of acetylcholine with a specific receptor protein is essential for the conductance changes observed [in the axon]. The agent that propagates impulses in the axon and across the synapse is the electric current (ion movements) but the ion movements require the trigger action of acetylcholine [p. 241 of Nachmansohn and Neumann, 1975].

and

> Electric fields and manifestations must be greatly influenced by the complexity of this organization [of the synapse revealed by electron microscopy]. But there is not a single fact to support the view that the role of acetylcholine system present in both pre- and postsynaptic membranes differs fundamentally in axonal conduction and synaptic transmission. All data available are consistent with the unified concept [p. 256].

Even in 1975 his views about the synapses were essentially unchanged. "Special structural arrangements may make small eddy currents at junctions quite efficient in initiating the chemical reactions responsible for the changes in the postsynaptic membrane for either hyper- or depolarization" (p. 197).

I have never understood why Nachmansohn was so resistant to the idea of chemical transmission, which would have been permitted by very minor modifications of his view of the role of acetylcholine. Perhaps some of the evidence for its role in axonal conduction would have been undermined if interpreted as associated with chemical transmission. Alternately his tenacity in support of electrical transmission may have been simply another facet of the personality trait that led him to hold an unpopular and finally indefensible theory of axonal conduction.

Many other scientists have held on to their theories for longer than they were tenable. In spite of Occam's razor a pet theory can often be nurtured by subsidiary hypotheses far beyond the point where the proposer would have been likely to formulate the theory *ab initio*. Simplicity is a useful guide in formulating theories, but once a theory becomes a member of one's inner family, the drive towards simplicity has a way of losing its strength.

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MARINE BOTANY AND ECOLOGY AT STAZIONE ZOOLOGICA

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Abstract

For 108 years marine botany research has been an important component of the research conducted at the Stazione Zoologica of Naples. The first researchers at the Naples Institute were German guests who proceeded with descriptive ecological and taxonomic studies and provided a foundation for the later physiological, cytological, life cycle, and biochemical studies conducted at the Stazione. During a major period (47 yrs.) Prof. G. Funk contributed ecological work giving the botanical research at Naples a continuity which extended into the late 50's. From 1960 onwards, the marine botany laboratory assumed a different direction and recently has returned to a physiological-ecological orientation. The lasting impact of marine botany has been the contribution of an ecological dimension from which other studies grew and found support.

Discussion

Studies of marine botany in the Gulf of Naples predate the founding of the Stazione Zoologica by nearly fifty years. The studies of Delle Chiaje (1823) and Costa (1838) describe species of the rich flora found in the waters of the kingdom of Naples. This flora and the equally abundant and varied fauna were factors influencing Anton Dohrn in establishing the Naples Institute. Within four years of the opening of the Stazione Zoologica, marine botany research was begun in earnest. For the past 108 years, research in this discipline has continued to contribute to the overall scientific effort. Marine botany and ecology are natural synonyms for the Stazione Zoologica, since from the beginning the ecological approach to the study of marine algae predominated, resulting in quantification and evaluation of the evolution of Neapolitan coastal waters. In addition, algal studies relating to cytology, physiology, anatomy, and aspects of biochemistry were pursued. Both micro and macro algae were studied although the major emphasis was placed on macroscopic thallate forms. The activity of marine botany research was greatly influenced by the perturbations imposed by the two world wars as well as the natural rhythms of the Institution's growth.

The earliest visitors (1873–1900) were almost exclusively German researchers encouraged by Anton Dohrn to visit and work at his station. Among these, J. Reinke, P. Falkenberg, G. Berthold, R. Valiante, and C. Sauvageau were the first to extensively study the benthic algae of the Gulf. Armed with the modern elements of taxonomy and physiology, these early workers (Reinke, 1878a, b; Falkenberg, 1879, 1901; Berthold, 1882a, b; Valiante, 1883; Sauvageau, 1892) established vital species lists as well as distribution in the Naples area. In addition, their observations on gametes of brown algae, cellular composition including ions, chromoplasts, vacuoles, and associated membranes further added to the general knowledge of algae. The first decades of the 20th century had macroalgologists including A. Vickers, F. Tobler, E. Leick, and G. Funk as further contributors to our understanding of algal species distribution as related to ecological factors. Among these, the most

prominent and one who had the greatest impact on marine botany in Naples was G. Funk. Professor Funk's monographs (1927, 1955) with extensive descriptions of algal associations, reproductive cycles in nature, and distribution remained a benchmark for algal research in the Mediterranean. Funk's observations also served as a basis for quantifying changes in natural populations in the Gulf of Naples where increased urbanization and industrial development was strongly affecting coastal waters. An important aspect of his research was the sustained effort over a 47-year period of research at the Stazione which established a strong ecological perspective in the study of marine algae.

Microalgal studies concomitant with those mentioned above resulted in the establishment of new species lists for diatoms, dinoflagellates, and other flagellates. Castracane (1889), Shütt (1891, 1892), Schröder (1901), Karsten (1925), and Balsomo (1903) substantially added to the microalgal species discovered in the Gulf of Naples. Subsequent works of Lindemann (1924, 1925), Zimmerman (1930), Schussnig (1930), and Schwarz (1932) added further understanding of dinoflagellates and microflagellates of this area.

An understandable decline in activity preceeded and followed the wars but the decade prior to World War II marked a period of intense research with macro algae. Physiological studies dealing with temperature (Biebl, 1939), growth substances (Weij, 1933), osmotic relationships (Höfler, 1930, 1931, 1932), ion permeability (Brooks-Moldenhaur, 1932; Mägdefrau, 1933; Ullrich, 1933, 1934, 1936, 1939), and pigment composition (Rodio, 1926, 1929, 1939) were actively pursued. Life cycle studies, primarily with brown algae were reported by Carter (1927), Hoyt (1928), Knight (1929), Pantanelli (1923), and Ubisch (1928, 1931), and observations on sexual cycles and structures were published by Hartmann (1925, 1934, 1937), Jollos (1926), Föyn (1934a, b), and Moewus (1938). During this period both Hammerling (1934a, b) and Schulze (1939) pursued studies of *Acetabularia* species present in the local waters. These studies were part of the pioneering work which was pursued in their native Germany establishing *Acetabularia* as an important physiological model and tool in the studies of cell biology.

The years following the second world war saw few or no botanists at the Stazione. It was not until the early 50's that botanical studies resumed full activity in research, progressing with ecological studies of algal distribution, algal cultivation, and work dealing with various aspects of *Acetabularia* metabolism. In the late 1950s, a marked change occurred in the marine botany laboratory with the permanent assignment of Dr. Kurt Beth, of the Max Planck Institute, as head of the algal laboratory in Naples. As a cell physiologist, Dr. Beth was primarily interested in *Acetabularia* research (Beth, 1958; Thimann and Beth, 1959), ephiphytism (Beth and Merola, 1960), and reproductive cycles in *Halimeda tuna* (Beth, 1962). In 1963, Dr. Beth organized and hosted the First International Algal Conference at Naples.

With less emphasis on ecology, the botany efforts during the decade between 1960 and 1970 left open pressing questions and concerns regarding the study of the environment. As a result of this and other factors, the Benthic Ecology and Biological Oceanography laboratories were formed and pursued topics no longer conducted in marine botanical research. Ecological studies in the broad sense, including research on the physical-chemical factors as well as plant and animal communities, are now being conducted by the three laboratories.

Today marine botany has regained activity in both macro and micro forms combining a physiological-ecological approach to the study of algae. Population dynamics of micro algae, distribution and abundance of toxic and noxious forms,

and physiological requirements of open ocean species are but a few of the research interests added to the macro algal distribution and abundance studies. An active herbarium, consisting of 3000+ specimens dating from 1881 to the present continues to serve as an important reference for taxonomic and systematics studies. Activities involving international collaboration have resumed and expanded. Advanced-level international courses are currently being organized.

A lasting impact of the marine botanical activities during a century of research at the Stazione has been a continuum of ecologically oriented studies which served as a backbone for other research activities. This, primarily attributed to the efforts of Professor Funk, has served as a basis of what we find today as botany-ecology at the Stazione Zoologica.

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CARNEGIE INSTITUTION OF WASHINGTON AND MARINE BIOLOGY: NAPLES, WOODS HOLE, AND TORTUGAS

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INTRODUCTION

At 2:45 p.m. on 29 January 1902 the Board of Trustees of Carnegie Institution of Washington met at the State Department in Washington, DC under the temporary chairmanship of the honorable John Hay, with Charles D. Walcott serving as temporary secretary. Andrew Carnegie, who was introduced by the chairman, presented his deed, creating a trust for the benefit of the Carnegie Institution of Washington, DC. After adoption of the by-laws officers were elected, including the honorable Abram S. Hewitt as chairman, Dr. John S. Billings as vice-chairman, Walcott as secretary, and as the Institution's first president, Dr. Daniel C. Gilman, former president of the Johns Hopkins University.

The second meeting of the Board was held the following day at the New Willard Hotel in Washington. At that meeting an Executive Committee was elected, which was charged with "preparing a report upon the work which should be undertaken by the Carnegie Institution in the near future, such report to be submitted to the Board of Trustees at its next meeting—." To that end the Executive Committee appointed eighteen advisory committees, whose roles were defined in a letter from President Gilman to each advisor on 11 March 1902. These fifty individuals were "invited to act as one of these advisors until the Annual Meeting of the Trustees, in November next." The charge to the committees was "to prepare, in the course of the summer, a plan of procedure, and in the meantime to engage in preliminary studies of the problems committed to them, by consultation with acknowledged authorities at home and abroad."

Among the committees was the Committee on Zoology. Its chairman was Henry F. Osborn, the other members being Alexander Agassiz, W. K. Brooks, C. Hart Merriam, and E. B. Wilson.

The several Committees reported to the Trustees on 25 November 1902. Those reports appear in Carnegie Institution of Washington Yearbook, Volume 1.

The reports of several of the advisory committees are considered "classics" in their respective fields, perhaps the most far-reaching being a report of the Advisory Committee on Astronomy, which produced a veritable charter for work in astronomy over several decades and resulted immediately in the establishment of Mount Wilson Observatory. The report of the Committee on Zoology cannot be classified among the great reports of the group, in part because only three of the five members of the Committee took an active part in the deliberations. Agassiz withdrew from the Committee before it completed its deliberations, and Merriam did not attend the final critical meeting. Merriam was one of the first to argue that Carnegie Institution should be an operating, not a granting institution. He was opposed to any plan that would result in scattering the work and funds of the Institution. He believed that "existing institutions should be allowed to continue their work without aid or interference from the Carnegie Institution." He was "fully convinced that the Carnegie Institution should carry on its own work, under its own name, and should publish the results in its own series of publications."

The Zoology report was signed only by Osborn, Wilson, and Brooks. It must be noted that all were active members of the Corporation of the Marine Biological Laboratory. Thus it is not surprising that the Zoology report emphasized marine biology, treating it under four different headings.

In a section entitled "Permanent Advisory Committee" it was proposed that a permanent Advisory Committee on Zoology be established, on the rotation system, to act as advisors in connection with the Marine Biological Laboratory and Experimental Station, the encouragement of research, expeditions—and so forth. The reader will note that the title "Marine Biological Laboratory and Experimental Station" is capitalized.

Under a further heading, "Marine and Experimental Stations" the Committee strongly endorsed "the establishment of a permanent biological laboratory as a central station for marine biology in general, with branches at such other points as may seem desirable; also affiliated or independent experimental stations for the study of physiological zoology and problems relating to heredity, evolution, etc."

Under the heading "Subsidies," the Committee concluded that "the Zoological Station at Naples will in all probability be one of the most important centers for special research work. . . . It is therefore desirable, and this Committee strongly recommends, that the Carnegie Institution subscribe annually for a table at Naples to the value of $500. . . ."

Finally, under "Supplementary Notes" is found a minority report, a "note by E. B. Wilson" who argued that the Institution should support regularly *at least two tables* at Naples. Wilson wrote, "The advantages derived by American biology as a whole from the Naples station in the past has been of incalculable value. . . ."

Before proceeding, let me call attention to the striking differences in referring to marine biology under two headings, just a page apart. Under one heading the Committee spoke of "the Marine Biological Laboratory and Experimental Station," while under the other it wrote more generally of the establishment of a permanent laboratory "as a central station for marine biology in general. . . ." This disparity has special significance, and the reasons for it will be made clear. It is indeed the central part of our story. First, however, let me take up briefly the history of interactions between Carnegie Institution and the Stazione Zoologica.

Carnegie Institution and Stazione Zoologica, 1902–1924

E. B. Wilson's minority report prevailed with the Carnegie Executive Committee, which on 27 October 1902 recommended to the Trustees that the Institution subscribe to two tables, at a total annual cost of $1000. The Trustees approved and grant number 55 provided for two tables for the year 1903. One of the tables was occupied for three months during the spring by E. B. Wilson, and the other by H. S. Jennings (then at Michigan). The remainder of the year the tables were to be "open to whomever the director of the laboratory might wish to assign to them."

On 20 December 1902, Anton Dohrn wrote to President Gilman, thanking him for his "most desired Christmas present," and asking whether the two tables "will be a permanent establishment?" and whether Gilman wanted "a contract." To this, Gilman replied, on 5 January 1903, "I can only say that all our appropriations are made annually, and I have no authority to commit the Trustees beyond the present year. At the same time I can see no reason why they should not continue this appropriation for a term of years."

In fact, the Institution provided for two tables, without interruption, until 1915. In 1903, Wilson proposed that the Institution take a third table, but that request was denied and the level remained at two tables.

The Institution's final check for $1000 was sent to the Stazione on 28 January 1915, and was acknowledged by Reinhard Dohrn, then Director, on 15 February. The Carnegie files thereafter are not extensive. During World War I the Royal Italian Government assumed the "temporary and extraordinary administration" of the Stazione, and at the same time Carnegie Institution was involved deeply in science in the service of the United States.

Correspondence was resumed in 1919–1920. Inquiries were received from B. Harvey Carroll, the American Consul in Naples, from E. B. Wilson, and from William Treadwell, among others. The correspondence in the Carnegie Files reveals very little of the ferment in Naples at that time. In response to all of these inquiries, President Woodward declined to recommend to the Trustees that the Institution re-establish relations with the Stazione. On 27 March 1920, Woodward wrote to Wilson, "One of the rules we have followed since the foundation of the Institution is not to give funds to governments. . . ." This was to be the "established" or formal explanation for Woodward's decision. As Woodward wrote to Wilson, "Some months ago I informed the Italian authorities that the Institution would not be likely to give any aid to the Station so long as it is maintained as a governmental establishment."

The correspondence does reveal that Woodward as an individual was sympathetic to Reinhard Dohrn. The Institution's files contain no direct correspondence with the then Director of the Station, Professor Monticelli.

The question remained dormant until 1924 when further inquiries were received, including one from C. B. Davenport, Director of the Institution's own Department of Genetics. By this time John C. Merriam had succeeded Woodward as President. On 24 July 1924 Merriam's administrative secretary wrote, "I am sure that Dr. Merriam is desirous of cooperating in such a project if it proves possible to do so, but for the present the Executive Committee of the Institution has not considered that there are available funds for this purpose."

Here this story ends, but the ending should come as no surprise. The Institution was supporting its own struggling Department of Marine Biology, and financial exigencies were already pressing President John C. Merriam and the Trustees toward C. Hart Merriam's position that the Institution's "strength and influence should not be weakened by diluting and scattering its resources, but husbanded for uses in keeping with the promise and scope of the Institution."

Carnegie Institution and the Marine Biological Laboratory

We pick up our story again in 1901, not in Washington but in Woods Hole (or Woods Holl as it was then called). The Marine Biological Laboratory, then in its thirteenth year, was in grave financial difficulty. In the words of a committee chaired by Frank R. Lillie (and including C. M. Clapp, E. G. Gardiner, C. O. Whitman and E. B. Wilson), reporting to the Corporation of the Laboratory in the summer of 1902,

> For several years the financial needs of the Laboratory have been growing without any corresponding increase of income until the conditions became alarming. The Trustees had frequently been told by those to whom appeals for support were made that the defects of our business organization were deterrent to those who might otherwise contribute to its material support. This condition was brought to a crisis by an offer received by the Trustees before the last Annual Meeting of the Corporation, under which generous financial support was guaranteed provided a suitable business organization could be effected. It was to attain this end that

> the Trustees asked at the last Annual Meeting of the Corporation that the power of modifying the by-laws be entrusted to them. This power was given by a modification of the by-laws adopted at the Annual Meeting in August, 1901.
>
> The plan under consideration at that time involved the transfer of the property of the Laboratory to a small section of the present Board, composed of business men who were to assume full financial control and management, while the scientific members of the Board were to continue as an advisory scientific council, with general supervision of the work of the Laboratory. It was thus hoped to secure an efficient financial administration as well as large financial support, without sacrificing the independence of the Laboratory or the cooperative principle which has been so potent a factor in its success in the past.

This plan was adopted unanimously at a meeting of the Trustees of the Marine Biological Laboratory, held in Chicago, 2 January 1902, and it appeared that a fundamental change in the organization of the Laboratory would be effected that very year, requiring only ratification by the Trustees at a special meeting to be held in the state of Massachusetts.

But, as the Lillie Committee wrote, ". . . before ratification of this action, the announcement of the Carnegie Institution suggested the possibility that the great resources of this endowment might be made available for the support of the Laboratory."

This plan, which was never ratified, is described fully by F. R. Lillie as the "Chicago Plan" in his book *The Woods Hole Marine Biological Laboratory* (1944). It must be described here briefly because the controversy surrounding it helped to shape the environment in which the "Carnegie Plan" was debated.

On 2 August 1901 President W. R. Harper of the University of Chicago had written to the Laboratory's Director, C. O. Whitman (also a Professor at the University) to say that "a company of gentlemen, including Mr. A. C. Bartlett of Chicago, Mr. Charles Coolidge of Boston, Mr. C. R. Crane of Chicago, and Mr. L. L. Nunn of Telluride, Colorado" were prepared to become the Laboratory's Trustees, assuming full financial control and providing management (including a guarantee of ten thousand dollars in 1902), with the existing scientific Board assuming the new role of scientific advisors.

Why did the Chicago Plan fail? The projected special meeting of the Trustees was held, but only seven Trustees (barely a quorum) appeared, and the Director was absent.

As Lillie described it, there was hope of securing aid from Carnegie Institution. However there was apprehension as well. After all the plan emanated from, or was conveyed by, President Harper, and two of the key "players" were Whitman and Lillie, also at the University of Chicago. The Trustees clearly feared control by a single university. These fears were exacerbated by the fact that the new lay Trustees would include "in-laws" of both Whitman and Lillie.

Thus it is not surprising that the Laboratory's Trustees turned readily toward the fledgling Carnegie Institution, but they were not alone among marine biologists in their dream of tapping the Carnegie wealth. David Starr Jordan submitted a plan for studying the fish of the Pacific Ocean. Alexander Agassiz, then President of the National Academy of Sciences, proposed an expedition to the Pacific to study marine life. The Governor of Bermuda sought support for the marine station there. The Marine Biological Laboratory had one unique advantage, however, in the person of E. B. Wilson, a devoted "MBLer," and a member of Carnegie's Committee on Zoology, a staunch advocate of the establishment of a "permanent biological laboratory as a central station for marine biology in general." Moreover, Wilson

was not alone in his support of the Marine Biological Laboratory, for as we have already observed, both Brooks and Osborn served both the MBL and Carnegie.

Events moved quickly. Overtures were made by MBL Trustees to their counterparts at Carnegie, and a formal application for aid was sent to President Gilman. On 11 March 1902, on Walcott's motion, the Carnegie Executive Committee resolved that Dr. J. S. Billings be appointed a special committee of one to investigate and report upon the desirability of the Institution making a grant for the maintenance of the Marine Biological Laboratory. Billings conferred almost at once with Brooks, Osborn, Whitman, and Wilson, and as a result of that conference, stated his willingness to report favorably on the application. It should be emphasized that Billings made his own position clear at the outset: Carnegie would be more than a granting institution. He believed that the Institution should place the Laboratory on a permanent basis, purchase land, erect and equip a new laboratory, and make suitable provision for its maintenance. Moreover, if this maintenance were to be of a permanent character, he argued, Carnegie should be placed in full financial control of the property of the Laboratory.

Moreover, the level of support envisioned by Professor Wilson and other members of the MBL Board of Trustees was made clear to Billings, who wrote to President Gilman on 24 March 1902, "This will involve an expenditure of about $80,000 within the next three or four years . . . , and also an annual expenditure of about $30,000 for current expenses."

Finally, the Carnegie perspective on teaching was made clear as early as 13 March 1902, when Billings wrote to Wilson ". . . it should be understood that the primary object of the Laboratory is to promote original research and to give to competent persons an opportunity to make such research, and that it is not of the nature of a school for teaching ordinary students?"

As a result of the conference between Billings and the MBL group, a special meeting of the Board of Trustees of the Marine Biological Laboratory was called. At that meeting, held in New York, 22 March 1902, the Trustees approved the incorporation of the Marine Biological Laboratory by the Carnegie Institution "on the lines indicated in the letter of Dr. Billings," and called for the formation of a committee to work with the Executive Committee of Carnegie Institution. Carnegie responded almost immediately, following a meeting of its Executive Committee on 25 March 1902. It was resolved that Carnegie would acquire the Marine Biological Laboratory, with the understanding "that Trustees of the Laboratory are willing to turn over its plant to the Institution, provided the latter will undertake the maintenance and support of the Laboratory." The Carnegie Trustees envisioned that the MBL would become the Institution's "Department of Marine Zoology." A special committee was formed by Carnegie to work with an MBL Committee to prepare a detailed plan for the organization of the new department. Moreover, to help the MBL through its difficult times, the Executive Committee resolved to provide the sum of $4,000 on or after 1 August 1902 as a first contribution toward the expenses of the Laboratory—providing satisfactory evidence was furnished "that the Trustees of the Marine Biological Laboratory have full power to transfer the property of the Laboratory to the Institution, and have agreed to do so."

Two joint meetings of the Conference Committee were held in April and May. Now, second thoughts began to emerge.

The MBL was in a state of ferment—in crisis—and looked to Carnegie (as it had looked to the Chicago group) as its financial savior. I emphasize the word "financial." The financial crisis was real, yet Whitman played only a small part in the early discussions with Carnegie. It was Wilson to whom most of the Carnegie

correspondence was directed. Wilson appears to have understood and to have accepted the Carnegie position. Whitman surely understood it—but he did not accept it; still he did not oppose it openly. On 10 May 1902, Wilson wrote to Walcott as follows:

> In reply to your letter of May 3rd: I shall be glad to make a number of suggestions regarding marine biological research in case the Wood's Hole plan is not carried out, but I hope that there is no danger of this plan failing. The only difficulty with the plan seems to be that Professor Whitman is reluctant to take any steps which will not unite the support of the Carnegie Institution with that of Messrs. Crane, Nunn and others. The rest of us feel that the plan embodied in the sketch of by-laws that has been drawn up in consultation with Messrs. Billings and Hewitt ought to insure this and probably will, and I trust there will be no difficulty in making the transfer of the property.

Carnegie, too, was in ferment, but its ferment was of a different kind. Andrew Carnegie had decided not to found a national university, but to establish an institution devoted to pioneering research and research training, not college or university education. Its Trustees were of several minds, however, as to the way Mr. Carnegie's mandate should be followed. Should all of the Institution's funds be devoted to its own operating departments, for which there were large demands from the very beginning? Should the Institution be primarily a granting agency, and if so, should the recipients of grants be established institutions, or individuals? It was many years before the question was fully resolved, with the Institution focusing entirely on operating its own departments. In 1902, however two trends had already begun to emerge, the formation of new operating departments, and grants to exceptional individuals. The idea of providing substantial grants on a long-term basis to existing organizations found less favor. The proposal by the Marine Biological Laboratory provided the first great test for the Carnegie Trustees on this question.

The test began with a proposal from the Laboratory that a *joint* Board of Trustees be established, equally representing Carnegie and the existing Board of the Marine Biological Laboratory. This proposition failed, with the Carnegie representatives stating, in substance, that it was not the Institution's policy to enter into alliance with existing institutions in such a manner as to involve divided control. The Carnegie group made clear that the Institution might, from time to time, make special grants to the Marine Biological Laboratory (as it might to other institutions or individuals) but that permanent and continuous support could only be promised on condition of a definite and complete transfer of property to the Institution, so that it might assume full financial control and responsibility. They stated positively at that time, and subsequently, that it was the wish and intention of Carnegie Institution upon assuming control, to give "the managers" the fullest possible scientific independence and freedom.

In due course, the Conference Committee finally agreed to amend the by-laws of the Marine Biological Laboratory to permit the transfer of the Laboratory to the Institution. The new by-laws were conveyed to the MBL Trustees on 19 July 1902.

The MBL would now constitute the Department of Marine Biology of Carnegie Institution. It would be under the general charge of a "Board of Managers," to be elected by the Executive Committee of Carnegie Institution. At the outset it was proposed that the Board of Managers would be composed of the then existing Board of Trustees at MBL. The Board of Managers would have immediate charge of the Laboratory, it would appoint the director of the Laboratory and in general would undertake all those responsibilities normally undertaken by the previous Board of

Trustees. However, changes in the by-laws had to be approved by the Executive Committee of the Trustees of Carnegie Institution.

On 12 August the Annual Meeting of the members of the Corporation of the Laboratory took what proponents of the transfer of the Laboratory to Carnegie might have regarded as final and conclusive action. The proposed by-laws to be enacted by Carnegie were read and explained to the Corporation. The Corporation was apprised that at the MBL Trustees meeting on 19 July a deed was approved that would convey to Carnegie the land and other holdings of the MBL Corporation. At the meeting of the Corporation, by a majority of over 60, it was voted that the Treasurer be authorized to execute, acknowledge, and deliver, in the name and in behalf of the Corporation the deed conveying all title to the Institution. Only three negative votes were cast, including one by an individual who would submit a competing proposal to the Institution, C. B. Davenport. All that remained then was for the Marine Biological Laboratory to report upon its needs and plans. Still another committee was empanelled, this time chaired by Whitman. Although Whitman had voted for the transfer at the meeting of the Corporation, he had let it be known that he favored an alternate course, namely of getting as large a grant as possible from the Institution, but remaining independent of it. Indeed, as Wilson indicated in his letter of 10 May, Whitman wanted monies from *both* the Carnegie and Chicago sources, but above all, he wanted the Laboratory's independence, which he then set out to ensure. Both he and J. McKeen Cattell (who had cast one of the three negative votes) published articles in *Science* calling the Corporation's action into question. Whitman's article, "The impending crisis in the history of the Marine Biological Laboratory" (1902) is especially noteworthy. Moreover his Committee report, presented as a "Report of the Trustees of the Marine Biological Laboratory to the Trustees of the Carnegie Institution" called for an effort far beyond the scope proposed by Carnegie at the outset. Moreover, surprising especially to those who have known the Marine Biological Laboratory in recent decades, when a premium was placed on working with marine organisms, is the statement that "Biological Station" would better express the character and aim then did the name, Marine Biological Laboratory. The report states in fact that the word "marine is there for a somewhat misleading reminiscence of an early stage of development, when sea forms alone occupied attention."

The report called for not only a "central station at Woods Hole" but also for secondary stations on the Maine coast and in the West Indies. It was stated further that "fresh water ponds" would be required as well. Finally, it was argued that a Biological Farm would be needed for studies of heredity and evolution (possibly to accommodate the needs of Davenport).

Charles Coolidge, a Boston architect, provided an estimate on the cost of buildings, land and equipment, which far exceeded anything discussed previously. According to this proposal the initial cost for a wharf, steam launch, buildings, ponds, apparatus etc. would amount to over $450,000. Maintenance costs were estimated at $30,000 for 1903, $75,000 for 1904, and $100,000 for 1905.

It is difficult to evaluate this Report without indulging in "psychohistory." There can be no doubt that it was prepared hurriedly, but even considering that, it is a rambling, poorly documented statement, not up to Whitman's usual standard—especially the long argument for a Biological Farm. The Committee had to have known that they were calling for far more than Carnegie intended to provide, that the proposal was unrealistic and doomed to fail. A "psychohistorian" could argue that Whitman had decided that if MBL were to lose its independence, it would be at a very high price. This report was prepared after 12 August and before 4 October

1902, for on the latter date the Carnegie Executive Committee considered it along with other information received, from MBL Trustees and others. By then, it was clear to the Carnegie Executive Committee that despite the MBL Corporation's definitive action, there was still substantial unrest at the Laboratory. The Carnegie Executive Committee felt constrained to inform MBL of the general principles that would govern the Executive Committee in its recommendations to the Carnegie Board in November.

The Carnegie Executive Committee reiterated that it would have to be distinctly understood that in the case of difference of opinion as to expenditures to be made or liabilities to be incurred, or as to the policy to be pursued in the conduct of the Laboratory, the decision of Carnegie Institution, after proper hearing of the views of the managers to the Laboratory, shall be final and conclusive.

Moreover, the Executive Committee reiterated Billing's statement of 24 March 1902, that the Laboratory should be used for research and not for teaching and that no instruction shall be given except such as may be furnished by investigators to their assistants. The object should be to provide "competent investigators with facilities for making researches."

Moreover, the scheme proposed by the MBL Trustees of making the MBL an institution for the investigation of problems of evolution, heredity, etc., including a Biological Farm, would not be approved.

Finally, the Executive Committee reiterated that it would not recommend more than $80,000 for land, buildings, etc., spread over the first two years; moreover, it would recommend $10,000 a year for maintenance. Finally, in a crucial statement, the Executive Committee concluded

> if, after considering these statements, the Board of Trustees (of the Marine Biological Laboratory) is of the opinion that it would prefer to retain the independence of the Laboratory, as urged by the present Director (Whitman), and not turn over its property to the Carnegie Institution, the Executive Committee is prepared to consider a proposition for granting aid to the Laboratory to the amount of $10,000 a year for the next three years, on condition that twenty research tables be placed at the disposal of Carnegie Institution, the occupant of each table to be furnished with supplies and material substantially as is done by the Naples laboratory.

The Executive Committee asked the MBL Trustees to respond by 25 October 1902.

The Carnegie offer of a significant grant for three years was exactly what Whitman had been seeking. He was quick to move, convening a meeting of the Executive Committee of the Marine Biological Laboratory to reply to the Carnegie Executive Committee's resolutions. Two reports were submitted by the MBL Executive Committee, a majority report, signed by three members of the committee, Whitman, Lillie, and Jacob Reighard; and a minority report signed by E. B. Wilson and T. H. Morgan. The majority report stated that in its view the general principles stated by the Carnegie Executive Committee were "in some essential respects so different from anything that has been hitherto considered by the Corporation and Trustees of the Marine Biological Laboratory, that they would not feel justified in authorizing the transfer of the property . . . without adequate reconsideration by that body and the Trustees." They therefore stated their opinion that the MBL should retain its independence, and requested a grant of $10,000 a year for a period of three years.

The minority report agreed with the majority of the committee that the transfer of the Laboratory to the Institution "is for the present inexpedient." They were

very explicit however in stating that they held this opinion not because they regarded the Carnegie recommendations as essentially different from the earlier plan, but "because the Director of the Laboratory has come to doubt the desirability of that plan." They stated further "we do not agree with the Director's view, but consider the transfer of the Laboratory inexpedient unless practically unanimous action can be taken." Thus the minority view argued that the wisest course is "to recommend application for a grant of $10,000 for one or more years . . . until the situation may become more clearly defined."

Wilson and Morgan went on to express the hope that Carnegie Institution may "without detriment to the interests of the work at Woods Hole, establish or support a marine station or stations, devoted to pure research, at such points as may seem desirable."

Neither minutes nor correspondence reveal disappointment on the Carnegie side, even though the record clearly shows that the final Carnegie position differed hardly at all from the recommendations advanced by Billings six months earlier. MBL knew what Carnegie had in mind (Wilson's letter of 10 May to Walcott), but Whitman, undoubtedly stung by the earlier criticisms he had suffered because of the "Chicago plan," held stubbornly to his vision of independence, and outmaneuvered (or perhaps better, outlasted) Wilson. The Carnegie position was clear: its Executive Committee had offered the MBL two propositions and one had been accepted. Nothing more need be said.

It is clear that on the MBL side not only Wilson and Morgan, but others were disappointed. Davenport was not. Carnegie provided, as agreed, $10,000 annually for three years. In 1905 Frank Lillie applied for continuation of aid for the laboratory for the next ten years, or indefinitely. On 23 January 1906, President Woodward responded, "I regret to state that after careful consideration it was decided that your petition may not be granted."

Carnegie Institution's Year Book Number 3 (1904) announced the establishment of a Department of Experimental Biology, including a Station for Experimental Evolution at Cold Spring Harbor, New York, to be directed by Charles B. Davenport, and a Marine Biological Laboratory at the Dry Tortugas, Florida, directed by Alfred G. Mayer.

The Station for Experimental Evolution, combined with Carnegie's Eugenics Record Office, differentiated gradually into the Department of Genetics, which provided some of the most glorious chapters in the history of that subject, capped by a period in which the principal scientists in residence included Hershey, McClintock, Demerec, Kaufmann, and Streisinger, among others.

Although Mayer himself was a man of exceptional promise, whose contributions loomed large at the time, the history of the Laboratory at Dry Tortugas was less glorious. It is the subject of our final chapter.

Carnegie Institution's Department of Marine Biology

The Board of Trustees of Carnegie Institution, encouraged further by the Committee on Zoology, continued to give marine biology high priority. Undaunted by the failure of negotiations with the Marine Biological Laboratory (and much to the relief of some of their advisors, and some members of the Board itself) they turned in a new direction. Andrew Carnegie, and the Trustees, had emphasized that the Institution should seek out and encourage the exceptional individual. An early "model" of the development of a truly outstanding department, arising from the brilliance and indomitable energy of one man, was the Department of Astronomy,

forged by George Ellery Hale. Encouraged by this model, the Institution turned to Alfred G. Mayer, a marine biologist and biological oceanographer, then just 36 years old. By all accounts, Mayer was indeed an attractive individual. The son of a distinguished experimental physicist, Mayer had early on forsaken his father's field to study biology, encouraged by Alexander Agassiz, with whom he had collaborated. Mayer, then a curator at the Brooklyn Institute of Arts and Sciences, was already an established investigator and prolific author, and he remained highly productive for the next eighteen years of his brief life. He was a naturalist, systematist, and comparative physiologist, as well as a superb sailor and a gifted amateur engineer and artist. Using the Laboratory's yachts, *Physalia* and *Anton Dohrn*, he studied the fauna along the Atlantic coast, and in other vessels made expeditions to the Pacific. He wrote about the growth of coral. He was deeply interested in the phenomenon of rhythmical pulsation in marine organisms—in the medusa, in the branchial arms of the barnacle, in the heart of *Salpa*, and of the embryo Logger Head turtle. He had a continuing interest in the swarming of the Atlantic Palolo worm. Despite the breadth of his interests, he explored a number of problems in such depth that he was elected to the National Academy of Sciences at the age of 48.

But if the Trustees selected a brilliant man to head the fledgling department, they allowed him to select a poor site for the Laboratory—Logger Head Key, Tortugas, Florida. From the beginning the Laboratory was seen to have two functions, to provide a base for Mayer's own expeditions and experimental studies, and to provide a setting for intensive research during the summer by university scientists. Unfortunately, the "season" was brief, from May through July when the hurricane season began. Tortugas, and the Laboratory as Mayer developed it, did not support families and a diverse summer community like that at the Marine Biological Laboratory. The number of visiting investigators was small, but the quality was high. In 1905, for example, the roster included E. G. Conklin, H. S. Jennings, William K. Brooks, R. P. Cowles, and Jacob Reighard, with Davenport Hooker as scientific collector. In the first five years of operation, Mayer reported a total of 29 visiting scientists in residence.

From the beginning however, the Laboratory was beset by problems: great hurricanes, the necessity of bringing supplies, including potable water, from Key West, and the inability of the Laboratory to accommodate wives and children.

Thus, Mayer was lead to propose transferring the Laboratory to the Bahamas, to Maine, or to Jamaica. He had emphasized at the outset that he had erected portable laboratories suggesting that he never viewed Tortugas as a permanent site. None of Mayer's pleas engendered a favorable response from Washington.

World War I brought further difficulties. The government converted the *Anton Dohrn* into a patrol boat and Mayer taught navigation and seamanship. And as Frank Portugal has written (unpubl. ms.),

> this was an equally unhappy period for Mayer. Strong anti-German sentiment in America made him ashamed of his German name. An embarrassed Mayer had such difficulties in getting his passport renewed that he had to ask Woodward for letters of recommendation attesting to his loyalty as an American citizen. Later, when he arrived back in America, he was subject to an intensive search by immigration officials, who labeled him a "suspicious character" and suggested that he carried wireless equipment for secret transmissions to the enemy. He had no choice. Writing Woodward, he announced, "my name has been legally changed from Mayer (a Hun name) to Mayor . . . the old form makes me bristle whenever I look at it.

Problems continued to mount. Mayor had tuberculosis, and another hurricane in 1919 severely damaged the facility. Mayor's death in 1922 from tuberculosis sounded the death knell for the Laboratory itself, although the Laboratory's death was "lingering." John C. Merriam, who had replaced Woodward as President of the Institution, had little interest in the Laboratory himself and found no support for it among other leading biologists in the Institution. The Trustees considered successors to Mayor including Alfred Redfield, then an assistant professor in the Harvard Medical School, but finally decided to perpetuate the Laboratory only as a modest center for the work of investigators for other institutions. Thus, instead of naming a new director, they named William H. Longley of Goucher College as Administrative Officer. All through the 1930s Merriam and the Trustees vacillated about closing the Laboratory. When Longley died in 1937 David Tennent of Bryn Mawr was asked to succeed him on an interim basis.

Vannevar Bush, who succeeded Merriam as President in 1939, settled the issue quickly. He closed the Laboratory and repaired the *Anton Dohrn* and transported it to the Woods Hole Oceanographic Institution.

Thus the dreams of Alfred G. Mayor, and of the Institution's 1902 Committee on Zoology were never fully realized, for marine biology was one of the few fields upon which the Institution embarked in which its efforts did not truly "make a lasting difference."

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[1] I have drawn heavily on Carnegie Institution of Washington Year Books, and on the Institution's Archives.

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EVOLVING INSTITUTIONAL PATTERNS FOR EXCELLENCE: A BRIEF COMPARISON OF THE ORGANIZATION AND MANAGEMENT OF THE COLD SPRING HARBOR LABORATORY AND THE MARINE BIOLOGICAL LABORATORY

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Introduction

I was asked to compare the organization and management of the Cold Spring Harbor Laboratory and the Marine Biological Laboratory. I began with the MBL, which was better known to the participants in the symposium.

Marine Biological Laboratory

The crucial element in the organization of the Marine Biological Laboratory is the relationship between the Trustees and the members who constitute the Corporation, for, in F. R. Lillie's words "this has been a controlling factor in the history of the Marine Biological Laboratory. The members constituting the Corporation proper elect—usually from their own membership—the Trustees, who, in their turn, have the exclusive right to elect the members of the Corporation." (Lillie, 1944).

When the Laboratory was incorporated in March, 1888, seven Trustees were elected, one of whom, Alpheus Hyatt, was the first President. There were in addition a Secretary, a Treasurer, and a Clerk. Immediately after they were elected, the first Trustees elected forty-seven additional members of the Corporation. For several years thereafter it was the custom to elect to the Corporation all workers at the Laboratory who signified their willingness to become members. By 1894, according to Lillie, there were 304 regular members and 52 life members.

Gradually, over the years, the number of Trustees was increased—to eleven in 1889, to nineteen in 1891 (plus two members *ex-officio*), and in 1897 to twenty-four, divided into four classes of six each, with three members *ex-officio,* the Director, Assistant Director, and Clerk.

By the 1940s, the number of Trustees had grown to thirty-two, four classes of eight, plus five members *ex-officio,* the President and Vice-President of the Corporation, the Director, Treasurer, and Clerk. With rare exceptions, all of the Officers and Trustees were scientists.

This pattern did not change significantly until the 1960s. In 1963 the by-laws were amended, adding a Chairman of the Board of Trustees to the already existing President and Director. The responsibilities of the Chairman and President were sharply defined, with the Chairman (a non-scientist) being responsible for business and external affairs, while the President, a scientist, would provide oversight, along with the Director, over scientific matters. The first Chairman was Gerard Swope, Jr., and the President and Director at that time were Arthur Parpart and Philip Armstrong, respectively. Later in the 1960s the number of Trustees was increased to thirty-six, with the additional Trustee in each class being a non-scientist, or "lay" Trustee.

In the 1970s, as the Laboratory moved further toward functioning as a year round scientific center, further changes in governance were required, and the composition of the Board of Trustees was changed again, evolving to the pattern of the current Board, twenty-four scientific Trustees, six in each class, elected by the Corporation, plus twelve "lay" or "Board" Trustees, three in each class, elected by the Board of Trustees.

Since 1970, the roles of President and Director have always been filled by the same individual, except for 1975–1976 when K. R. Porter was Director, with J. D. Ebert serving as President.

Authority to act for the Board of Trustees between meetings is vested in the Executive Committee of the Board of Trustees, composed of the officers of the Board plus six members elected by the Board of Trustees.

Cold Spring Harbor Laboratory

I turn now to the governance and major affiliations of the Cold Spring Harbor Laboratory.

It may be instructive, before examining the present organization, to take up briefly the origins of the Laboratory.

In the mid-19th century, John H. Jones built a dock to facilitate the outfitting of whale-ships on the east side of the inner harbor of the Long Island village of Cold Spring Harbor. His son, John D. Jones, inherited the family homestead and adjoining grounds. John D. Jones was an uncommon man of his day, who developed a keen interest in science. In the words of his brother, W. R. T. Jones (1904),

> the Brooklyn Institute [of Arts and Sciences] desiring a place to establish a school of biology, he [John D. Jones] put up for that Institute a building suitable for its purpose, and the school, under charge of able professors, has been a success, doing original work which has been a credit to Long Island, and acknowledged as such by similar foreign institutions. He also leased to the State of New York grounds for a fish hatchery, which is now turning out each year several hundred thousand trout and salmon to stock the inland waters of the State.

Thus science at Cold Spring Harbor sprung in large part from the interest of an exceptional individual.

Seeing the need of an organization to perpetuate the management and care of the grounds and property devoted by him to scientific research, John D. Jones incorporated the Wawepex Society, the name Wawepex being taken from an old Indian name of the harbor. John D. Jones was the first governor of the Society, continuing in that office until his death in 1895.

The next significant change at Cold Spring Harbor was the opening of Carnegie Institution of Washington's Station for Experimental Evolution on 11 June 1904, under the leadership of C. B. Davenport. The Wawepex Society offered about ten acres of land, which would be leased for fifty years to Carnegie Institution of Washington for a nominal sum. For twenty years the Carnegie Department and the Biological Station of the Brooklyn Institute of Arts and Sciences lived side by side. The Station for Experimental Evolution was combined with Carnegie's Eugenics Record Office in 1921 to form a Department of Genetics. Davenport remained Director until 1934, when he was succeeded by A. F. Blakeslee, who served in that role until 1941.

In 1924 the Brooklyn Institute withdrew its support of the Biological Station, and community leaders in Cold Spring Harbor organized their own association, the

Long Island Biological Association, that actually administered the Laboratory until its reorganization as an independent unit in 1962.

Although significant work had been accomplished at Cold Spring Harbor from the very beginning, the first "truly great" period in research there began with the arrival of Milislav Demerec at the Carnegie Department of Genetics in 1941. The two decades, 1942–1962, were extraordinarily rich in both the Carnegie Department of Genetics and the Biological Laboratory, managed by LIBA. The two organizations collaborated closely, and for a considerable period Demerec served as Director of both organizations.

In 1962 the Carnegie Department of Genetics was terminated as a separate administrative unit of the Institution. Those of its staff who remained at Cold Spring Harbor in the "Genetics Research Unit" cooperated with the new Cold Spring Harbor Laboratory that emerged from the Biological Laboratory in that year. As described in the Annual Report of the Cold Spring Harbor Laboratory, LIBA remains a non-profit organization, which represents a growing constituency of "friends of the Laboratory."

The current Board of Trustees of the Cold Spring Harbor Laboratory is divided between individual Trustees and "institutional" Trustees. Institutional Trustees—currently there are representatives of twelve institutions, including LIBA and the Wawepex Society—were brought on to the Board during the 1960s when the Laboratory was undergoing reorganization. The current Annual Report of the Laboratory states that

> in addition to supplying scientific leadership to the governing body, participating institutions also provided emergency funds to help keep the Laboratory afloat during this crucial phase of development. Although participating institutions now give only token financial support, their Trustees continue to help steer the course of the laboratory's scientific and administrative policies.

There are in addition thirteen individual Trustees; thus all told there are twenty-five Trustees, who meet three or four times a year. Again, authority to act for the Board between meetings is vested in the Executive Committee of the Board, which is composed of officers of the Board plus members elected to the Executive Committee by the Board of Trustees.

Crucial Differences

There are two crucial differences in the organizations of the Cold Spring Harbor Laboratory and the Marine Biological Laboratory. They are found in the existence of the MBL Corporation, and in the substantial majority of scientific Trustees elected by the Corporation at MBL. As Gross has written (1984), these are "working members of the faculty; dedicated scholars. They are specifically *not* outsiders. They have a high personal stake in the day to day operations of the place."

At Cold Spring Harbor, other than in the legal sense, there is nothing equivalent to the MBL Corporation. Control of the Laboratory is vested in the Board of Trustees, with the individual Trustees having a slight majority. However, that majority appears to have little significance, for the institutional Trustees nominated by the participating institutions and who rarely have a personal stake in the Laboratory's day to day operations, tend to act in concert with the individual Trustees.

From these significant differences in organization spring further differences in management, in both policy and style, expressed in the expectations of many MBL

Corporation members and Trustees to preserve and enhance "their own piece of the action." The uniqueness of the MBL's organization has not prevented the evolution of the Laboratory into a financially viable and creative modern center for research and advanced teaching, but at times it has slowed the process significantly.

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FIRST IMPRESSIONS: AMERICAN BIOLOGISTS AT NAPLES

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Abstract

This paper examines reactions of American biologists who traveled to the Stazione Zoologica in Naples during the 1880s and 1890s. The 1890s took a number of Americans to Naples despite the development of research resources in their own country. In part this can be attributed to the continued support of the Stazione by those Americans who had first gone, particularly by Whitman, Wilson, and Morgan. The Naples Station continued to exert an important influence on American biologists into the first years of the twentieth century.

Discussion

In 1881, Professor William Keith Brooks at Johns Hopkins reported that E. B. Wilson's dissertation work would make just as "valuable and handsome a paper as those from Dohrn's laboratory," if only a place could be found to publish it (Brooks, 4 June 1881). This statement revealed two phenomena: first, that the United States did not offer acceptable vehicles for publication of detailed biological work and second, that work at Dohrn's laboratory set a standard for biology by 1881. I wish to focus here on the second of these points. By 1881, the Naples Station had achieved a reputation in the United States for publication and research, but no American student had yet worked there. That situation changed when Charles Otis Whitman arrived in November 1881.

Presumably Whitman had heard about the Station while he was a graduate student studying under Rudolf Leuckart in Leipzig, but his first opportunity to visit Naples came after his three years of teaching at the University of Tokyo (Lillie, 1911; Morse, 1912). On his way back to the United States, he stopped in Naples, hoping to stay a few months. Since he had worked in Germany and since no institution from the United States had subscribed to a table at the Naples Station, Anton Dohrn welcomed Whitman as his guest from November until May 1882 (Lillie, 1911, p. xxiv). Whitman wrote to a friend that he was "having a delightful time at work in the station," and that he found there "greater advantages than are to be found anywhere else in Europe" (Whitman, 23 February 1892). While he had concentrated on leeches in Leipzig and Japan, in Naples he turned to the parasitic dicyemids (Whitman, 1883). Whitman recorded his positive reaction to Naples and Dohrn's Station in an article in *Science*, concluding that the international character of the Station had made it the "Mecca of biologists, and a seat of unprecedented prolific activity." Naples was the place to learn methods, Whitman wrote, and

> This one but all-important matter, to say nothing of the many other advantages that must accrue to an occupant of a table at the station,—such as social intercourse, direct knowledge of a very important fauna, and opportunities of acquiring a knowledge of the four languages with which every naturalist must now be familiar,—makes it very desirable, particularly for our younger naturalists, to spend some time at Naples [Whitman, 1883, pp. 94, 95; 1882].

He continued to call for American support of the Station, arguing that even if the

United States had its own laboratory (namely the United States Fish Commission), Naples offered special opportunities.

Another American visited Naples very shortly after Whitman left, as revealed by the records at Naples. Christiane Groeben has compiled a list of those Americans who visited Naples and has identified a number of items in the Archives at Naples for some of those individuals. Groeben reports that Emily Nunn was the second to visit the Naples Station. She had been studying in England and worked at an English table. She later married Whitman, though they did not meet in Naples. Emily Nunn recorded her favorable impressions of the Station, but evidently was advised to gain more experience in independent research before spending more time at Naples so did not stay as long as she had intended (Nunn, 1883; Groeben, 1984). Whitman was certainly the more important American visitor as far as Dohrn was concerned.

That Whitman left a very favorable impression on Dohrn is clear from Dohrn's letter supporting Whitman's application for a position at Columbia University. As Dohrn wrote, "The half year you worked in the Zoological Station has given me the highest opinion of what you will be able to accomplish in the right situation; and if my word can have the least influence with the authorities of the College, it will go thoroughly in your favor" (Dohrn, 25 June, 1885). Columbia did not, in fact, hire Whitman for that position but instead eventually chose Edmund Beecher Wilson for a similar job. And Wilson was the first man to work at the Naples Station officially, that is at a properly subscribed table (Osborn, 1895; Groeben, 1984).

At first Wilson encountered difficulties in receiving acceptance to work at the Station. He had expected to work at one of the English tables but found them full when he arrived in Naples in March 1883. Also he learned that "it is considered unfair to admit men to the station unless regularly provided for by a subscription from their own country." Even the prospect of a subscription would allow Dohrn to admit Wilson, but acting otherwise would be unfair to those of other countries whom Dohrn had had to turn away. Naturally, Wilson felt keenly disappointed, for he believed that "the station has now become practically the headquarters from which most of the leading European laboratories derive their best methods, and where, indeed, much of their most telling work is done." Naples remained a "tempting treasure" to be anticipated (Wilson, 9 March 1883). Fortunately, by April Wilson was in place at a table subscribed by Williams College in an arrangement made by Wilson's cousin Samuel Clarke, who went to Naples the next year while Wilson taught at Williams for him (Morgan, 1940, p. 126; 1941, pp. 319–320; 1942, p. 240).

In the meantime President Gilman of Hopkins had offered to take a table for Wilson, and Wilson, "as a good Hopkins man," regretted that Hopkins had not been the first American institution to do so. In part hoping to elicit Gilman's further support, Wilson enthused about the opportunities at Naples:

> It is in every respect the best laboratory I have seen and my high expectations have been fully met.
>
> Two things especially strike me as characteristic of this laboratory. The first is the perfection of the technical methods of research. It is now almost proverbial for zoologists to say: "For methods go to Naples" and in the same breath is usually added "A good method is half the battle." Certain it is that many of the best modes of work now used at Leipsic, Cambridge and elsewhere have originated here. The secret of this is simply that fifteen or twenty zoologists are usually at work, who come from laboratories in all parts of the world and bring

> their experience to a focus here. They are all experimenting and comparing results and new methods can thus be very thoroughly tested . . . [Wilson, 13 April 1883].

Wilson expected to stay awhile, possibly as long as a year in Naples, though he was not sure that he could afford such a lengthy visit. Yet Dohrn reportedly soon invited Wilson to stay for three years and to publish a lengthy study of the local *Renilla* which would complement Wilson's study of American *Renilla* (Brooks, 15 July 1882). Wilson loved the Station, the colorful setting, and especially the music which played an important part in his life. For family and career reasons, he nonetheless reluctantly declined Dohrn's offer and returned to the United States. As he said later, Naples had made "a deep and lasting impression" on him (Morgan, 1941, pp. 319–320). In discussing future plans for the Marine Biological Laboratory in later years, it is clear that Wilson retained fond admiration for the Naples Station and in some respects wished to make the MBL more like Naples (Lillie Papers).

A decade later, in the 1890's, Wilson returned for a second visit, along with an increasing number of other Americans. Undoubtedly the enthusiasm expressed by Whitman and Wilson during the summers at the MBL, as well as the exciting new work issuing from the Station stimulated a number of American biologists, including George Howard Parker, William Morton Wheeler, Thomas Hunt Morgan, and eventually Edwin Grant Conklin, to visit Naples themselves. The Naples experience influenced each of these men, as each directly responded to the dominant questions and research of Naples in his own work. Each of these men recorded the impressions which the Naples experience left on him.

Parker arrived first, in the spring of 1893. He had spent three summers in Woods Hole at the U. S. Fish Commission and the MBL, and then had gone to Europe to study the origins of the nervous system. He resolved to spend a half year each in Leipzig, Berlin, and Freiburg, then to go on to Naples, for as he said, "Every young zoologist of my generation was desirous, as part of his early training, to work at the Naples Zoological Station" (Parker, 1946, pp. 136, 82–83, 91). Though he did not say much about his scientific work at Naples, it seems clear that the opportunity to work with a variety of different organisms and to discuss results with a diverse group of researchers helped him to some of his generalizations about nervous structure and function. In leaving he concluded that "of all places to spend the opening half of the year Naples stood at the forefront" (Parker, 1946, p. 107).

Wheeler arrived in Naples at the turn of the new year, after a stay with Theodore Boveri in Würzburg. In a postcard to a friend at Chicago, Wheeler wrote:

> Have at last reached the "Mecca" and hope to go to work tomorrow, when my place in the lab will be ready for me. Naples is even more beautiful than I had imagined it to be. There is plenty of foliage on the trees and the weather is heavenly compared with what you are probably having in Chicago . . . Regards to the boys and to Professor Whitman [Evans and Evans, 1970, p. 89].

Yet Wheeler found the poverty and Neapolitan lifestyle appalling, even while he found the scenery so attractive. Though later known for his outstanding work on ants, Wheeler spent his time at Naples on developmental studies of various invertebrates, including the Myzostoma, which he found begin as small young males and mature into females. Clearly stimulated by the dominant concerns with development at the MBL and at the University of Chicago under Whitman, Wheeler's early researches followed the pattern of many of the young American biologists. His firm grounding in the methods and problems of cytology and developmental morphology provided the foundation for later work (Evans and

Evans, 1970, pp. 89–98). And he pursued that grounding during three and a half months of embryological study at Naples. Presumably it was at Naples that Wheeler became interested in the debates about development stimulated by the half embryo experiments of Roux and Driesch. Yet though he went on to translate Roux's manifesto for *Entwickelungsmechanik* for an evening lecture at the MBL, Wheeler always maintained a traditional morphological focus on the whole organism. He resisted the rush exemplified by *Entwickelungsmechanik* to cut up organisms and to manipulate them with experimentation. Leaving Europe in July to return to Chicago, Wheeler met Morgan, who was then on his way to Naples (Wheeler, 1895; Evans and Evans, 1970, pp. 104, 234–235).

Morgan clearly received a particularly strong stimulus to his work at Naples. Biographers have emphasized the contact there with Hans Driesch and Driesch's impact on Morgan (Allen, 1978). Clearly Morgan did respond to the debates in progress among Driesch, Roux, and others convened at Naples—debates about the extent to which an embryo experiences any preformation or predetermination because of its inheritance or early structure. Of the stimulating setting, Morgan wrote that "No one can fail to be impressed and to learn much in the clash of thought and criticism that must be present where such diverse elements come together" (Morgan, 1896). In fact Morgan's early work generally followed closely the interests of those around him or responded to problems which seemed particularly exciting at the time, so the stimulus at the MBL, then Naples directed him (Brooks, 21 June 1891). The years just prior to his Naples visit reveal his existing interest in the experimental work of Pflüger, Born, Roux, Chabry, Driesch, and Hertwig on early development: whether the concrescence theory works for teleosts and frogs and whether the echinoderm egg is isotropic dominated Morgan's work, with general questions about whether preformation or epigenesis best characterizes development. Much of Morgan's work began with a review and often the repetition of other results, then moved to Morgan's own related experiments. At Naples, where Morgan became friends with Driesch, his attention turned very directly to Driesch's work on fragmentation and partial embryos and their impact on interpretations of development. In the heated debate about preformation and epigenesis, about Weismann's and Roux's mosaic or Driesch's regulative views of development, Morgan himself maintained a moderate position, sympathetic to Driesch but closer to Whitman's emphasis on "organic continuity" to explain development (Sturtevant, 1959; Allen, 1978, pp. 55–60, 78–84).

Edwin Grant Conklin similarly rejected the developmental interpretations of Driesch or Weismann and Roux. His detailed cell lineage work on ascidian development led him to conclude that cleavage in some forms is determinate, in others indeterminate with respect to later development. This conclusion led him into direct disagreement with Driesch, who maintained that cleavage remains indeterminate. Yet when Driesch traveled to the United States he visited Conklin in Princeton and established friendly relations. It was not until 1910, when he attended a conference at Graz that Conklin visited Naples and followed up some of his disagreements with Driesch. Specifically, he examined at Naples the same organism that Driesch had studied there (*Phallusia mamillata*) and established that that form develops determinately as does *Cynthia* or *Amphioxus,* which Conklin had studied in detail earlier (Butler, 1952; Harvey, 1958, p. 65). He did not change his mind or his research program because of his work at Naples; rather his studies allowed him to discredit Driesch's alternative interpretations. And Conklin acquired further material to support his conclusion about the central role of cytoplasmic factors in development.

After the 1890's the American situation had substantially improved, and yet Americans still visited Naples. The MBL and the *Journal of Morphology* provided a laboratory and a publication outlet for Americans. And successful graduate programs provided places to pursue degrees. Yet the Americans went to Naples to learn theories and methods, to experience the special international exchange of ideas that took place at that "Mecca," and to examine organisms native to the area. The MBL did not replace the Naples experience for Americans and was not intended to do so, but complemented it. Positive first impressions stimulated a long tradition of American expeditions to the Naples Station.

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EARLY STRUGGLES AT THE MARINE BIOLOGICAL LABORATORY OVER MISSION AND MONEY

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Abstract

In its first decades, the MBL Trustees and their Director, Charles Otis Whitman, often disagreed over the proper goals and justified expenditures for the MBL. This paper examines the nature of those struggles and the attempts at resolution, leading ultimately to Whitman's disappointment and resignation.

Discussion

In 1884, before the MBL began, Edmund Beecher Wilson had spent a year in Europe after finishing his degree at Johns Hopkins. He wrote to President Gilman at Hopkins that a number of Europeans expressed surprise at the lack of interest in biology in America. So many organisms to be explored, so many resources to be developed. As Wilson wrote, "American zoology seems to me a good example of a prophet without honor in his own country" (Wilson, 13 April 1883). He continued to find it embarrassing that the United States lacked a permanent research facility. Baird's efforts at the United States Fish Commission had not succeeded in establishing it as a research center. There was room for an American laboratory, Wilson felt, and a need for one.

Naples offered a fine example of a biological research station, and for Wilson its superiority lay clearly in one simple fact: that "money has not been wanting, so that the management has been able to offer good facilities for work and has thus attracted the best workers" (Wilson, 13 April 1883). Of course, Dohrn deserves credit for supplying most of the money, and he worked continually to insure an adequate income at Naples. No one connected with the MBL offered as much as Dohrn did at Naples. Money remained a constant problem in the first decades of the MBL.

With only $10,000 for the first year, the MBL opened in the rather shoestring manner described by Cornelia Clapp (Clapp, 1927). The Trustees expected their money to prove sufficient for four years, then they planned to secure a permanent endowment (MBL *Minutes,* 1888). Over the first few years, they reluctantly authorized adding modest new buildings as the demand grew. Still, by the years 1892–1894 the MBL experienced a balanced budget, with the help of careful planning and cutting of extras, but 1894–1895 brought the beginning of serious crises (MBL *Minutes,* Annual Reports).

These financial troubles reflected more fundamental disagreements as well. The Trustees had not specified the goals of the MBL, for example, preferring instead to leave the definition to the first director. But they disagreed even about who should be that first director. Those Trustees from the Women's Education Association in Boston, who had supported the Annisquam precursor of the MBL, revealed their expectations from the beginning. Presumably they envisioned the MBL as following along more or less the lines that the Annisquam Laboratory had pursued, concentrating mainly on fairly introductory teaching. Thus they held that the director of

the MBL should be B. H. van Vleck, who had served as assistant at Annisquam. Other Trustees, including the Annisquam director Alpheus Hyatt, saw the advantages of selecting a nationally recognized figure like William Keith Brooks or Charles Otis Whitman, either of whom would bring major changes to the lab. In the end the Trustees chose Brooks, then Whitman. They left unspecified such major decisions as the relative roles they expected teaching and research to play, though the intention was always to pursue a balance of both unless the Fish Commission established a successful research center, in which case the MBL would focus on teaching classes (MBL *Minutes,* 1888, p. 38).

Beyond this basic agreement to pursue both teaching and research, however, the Trustees evidently never reached an agreement about the ways and degree to which they expected the MBL to expand. Thus, when Whitman insisted on making the expenditures he regarded as necessary to supply a legitimate laboratory for a growing number of people, the Trustees felt that Whitman spent too much. They sought to limit his spending (Whitman to Conklin, MBL *Minutes,* Annual Reports). Obviously, such disagreement led to fundamental struggles over who would control the MBL.

Whitman's contributions to the Annual Reports reflect his ambitions. The goal at the MBL should be "to organize one of the strongest and most productive biological stations in the world" which would allow the United States to make a good showing when compared with such successful places as the Naples Station (Whitman, Annual Report, 1890, p. 22). The MBL should remain a laboratory for all biology, including morphology and physiology, zoology and botany, marine and more general biology, and it should be a place for both independent research and teaching. For Whitman, the MBL promised to become the premier American biological laboratory. Yet he recognized the accuracy of Wilson's emphasis on money. He saw the need to obtain an endowment for the lab, ideally a half-million dollar endowment to establish a full-time, year-round biological station. His great hopes met continued obstacles, and the ideal of a permanent center for both research and teaching remained unrealized (Whitman, 1891, 1893a, b, 1894, 1898).

Success amplified the problems beginning in 1894 and 1895. Attendance had increased dramatically, from 15 in 1888 to 199 by 1895, and financing had become ever more difficult. To Whitman expansion seemed desirable, both for students and for researchers. He urged more building in 1895 to provide more room. And he continued to urge the need for solid financial backing. It looked, in 1895, as though that backing might materialize. Miss Helen Culver of Chicago evidently intended to give a half-million dollars each to the MBL and to the University of Chicago's biology program. Whitman headed both, and he worked hard to obtain the dual gift. A letter from Whitman to Miss Culver clearly indicates that part of the gift was originally intended for the MBL:

> The Marine Biological Laboratory has already become an intercollegiate centre for research and instruction. Some over twenty colleges and universities are now contributing to the support of the Laboratory by subscriptions to rooms and tables, and no less than eighty-five institutions were represented in our membership last summer. The national character of the Laboratory is the chief glory and that I am sure will be wisely guarded in the foundation you have bestowed.

Instead, for unknown reasons, Miss Culver gave the entire million to the University and none to the MBL (Whitman, to Miss Helen Culver, 20 December 1895). The goals for the MBL remained elusive.

Whitman continued to support growth and expansion, but in 1896 the Trustees as a whole said, in effect, "no more." Yet the Executive Committee of the Trustees

approved the expansion and expenditures. With Whitman's personal financial backing, the group finally achieved agreement, but the seed of crisis had been sown (Lillie, 1944, pp. 43–44; Trustees, 1897; Clarke *et al.*, 1897). The disagreement brought the first confrontation, with a major split in the Board of Trustees. In late 1896 and early 1897, the Trustees met and agreed to keep the lab open only if they could raise $2000 to cover costs. They met in Boston, and they did not even consult Whitman. Further, they postponed announcing the 1897 session until they had met and made financial decisions about whether to continue; the uncertainty cut into that summer's attendance. The annual meeting at Woods Hole in August 1897 was very tense, with major disagreements about how to run the lab. The meeting brought new by-laws and election of new Trustees, with only two of the original Boston Trustees remaining on the Board. As Whitman reported to Dohrn, he was particularly delighted to have gotten rid of the "old maids" from the Women's Educational Association who had no real connections with biology (Whitman, Naples, 2 September 1897). The new Board reflected greater national representation and greater biological commitment.

Yet financial troubles continued despite the greater ideological support from the Trustees. In 1898, Whitman wrote to his friend and supporter Edwin Grant Conklin that "I am having many sleepless hours over the lack of funds to pay bills this year. I have about resolved to take from my own poor pocket to settle the $600 unsettled salaries. I have reason to hesitate to do this, for I do not see the way out of it. Were it not for the many good hearts behind me, I should feel decidedly blue" (Whitman to Conklin, 1 November 1898). Indeed, a friend reported that Whitman had suffered very deeply from the troubles since the MBL was "the very apple of his eye" (Whitman, Chicago, 20 May 1898).

Whitman articulated ever more strongly that the United States needed a biological laboratory and that it should be a permanent station with a full endowment. Such a station must have national cooperation and must therefore remain financially and ideologically independent of any one group. Permanence, national support, cooperation, and independence—these became recurrent themes for Whitman (Whitman, Annual Report, 1890, pp. 22–23; Annual Report, 1892, pp. 29–36; 1893; 1901; to Morgan or Wilson, 1902). Without money, those ideals remained out of reach. At one point, however, the financial goal seemed nearly attainable.

In 1900 came a concerted effort to achieve wider national support from colleges to underwrite at least the cost of operations. Following the Naples model, the MBL did not try, in the early years, to extract more money from the individual researchers but appealed instead to institutions for more permanent support. Some, such as Alexander Agassiz, who had supported Naples and other efforts felt they had "thrown away enough money on seaside Laboratories" and balked at donating money to yet another attempt to build an American laboratory (Agassiz, 30 May 1888). Other colleges and institutions did continue to provide support. Finally in 1901 and 1902 two major offers came to relieve the Trustees of the bulk of their financial problems. The first came from four wealthy businessmen and was presented through President Harper of the University of Chicago. Whitman strongly supported their proposal and felt that it would secure the laboratory's financial independence and make realistic the establishment of a permanent research station (Whitman to Conklin, 1901 and 1902). Yet, though only two of the four men lived in Chicago, the Trustees felt that accepting the offer would give too much power to one university and that the lab would therefore lose the very independence and national character it sought. Whitman felt unsupported in the ensuing sometimes bitter

struggles, and he lamented to Conklin that though he felt confident that things would work out, presumably in favor of the plan, "I often regret that there has been such a strong sectional feeling in the East. It is *not* very pleasant to have ones motives impugned, and I confess, at times, to have found the suspicion against Chicago University and its men almost beyond endurance" (Whitman to Conklin, 2 March 1902). The fate of the Chicago plan remained unclear until a second offer came shortly thereafter leading to the rejection of the first proposal as such.

The second offer came from the Carnegie Institution and went through numerous revisions. The group most strongly supporting the Carnegie proposal included Wilson, who saw this as the chance to secure financial stability and to make over the MBL into a research lab more like his old ideal at Naples (Cattell, 1902, pp. 529–533; Lillie, 1944, p. 57; Whitman, MBL-Lillie, 8 and 13 October 1902). Wilson came into direct conflict with Whitman on this issue. It became clear to Whitman that while some of the Trustees, such as Conklin, remained firmly behind him, most had never really fully accepted his ideas for the lab. As Frank Lillie recorded later in his history, Whitman found it disillusioning to realize that there were "few who held with anything like equal intensity his belief that the ideals of organization for which he had fought were of value far superior to any degree of financial security" (Lillie, 1944, p. 60). Whitman feared that the Carnegie people would absorb the MBL as just another one of their own departments. He feared the proposed move to solely research and the loss of instruction which Wilson applauded. He suggested somewhat facetiously to Conklin that "Perhaps we had better abandon every class at Woods' Holl, and all compensation for *services*, and revert to the old-time ideal of a pure research station. I feel half inclined to do this, and so let everyone see by actual experience the result" (Whitman to Conklin, 7 January 1904). Obviously, he did not expect happy results.

Eventually, after much discussion and revision, a plan was developed by which the Carnegie Foundation supported the MBL for three years with $10,000 per year, matched by a gift from three of the Trustees—including some of the support offered in the first Chicago proposal—but the MBL Trustees and Corporation retained control of the lab. As an admirer put it later, Whitman had held firm for independence.

> Reportedly has Woods Hole declined riches when by its acceptance there is only the remotest possibility of interference with this indispensible independence. All of the proffers fell upon deaf ears. The nightingale may be captured, but it can never be made to breed by the huntsman nor be made to sing in confinement. It must live in its own peculiar habitat, and this is found for scientists in Woods Hole. In this country we are searching for heroes in productive science, but "the birds that may sing may seem to avoid the golden cage" [The Resignation, 1908, p. 382].

Nonetheless, Whitman felt defeated and exhausted and withdrew from the MBL. His assistant, Frank Lillie, took over the directorship (MBL Annual Report, 1908, pp. 8–13).

Whitman looked upon the struggles of 1902 as growing pains of sorts, in which the impatience of some had led to near disaster. As he put it, the MBL had begun like an organism, with only seventeen "ids in its protoplasmic body—two instructors, eight students, and seven investigators (all beginners). The two instructors could be likened, with no great stretch of the imagination, to two polar corpuscles, signifying little more than that the germ was a fertile one, and prepared to begin its preordained course of development." The original incorporators, Whitman said, served as

sponsors and left the group of ids to follow its own course of development. The germ thus underwent various cleavages and took shape. Founded on the principles of cooperation and independence, it sought to embrace all of biology. It even grew and advanced to the tadpole stage, Whitman reported. But some members wanted to shed their tails and become frogs, and to undergo that change immediately. They forgot the golden motto of development, proceed slowly. Fortunately, the supporters made it possible for the tadpoles to advance without loss of their heads as well as their tails. But do not forget the lesson, Whitman urged, for "There is a work before you of far greater magnitude and importance than perhaps any of us can now realize, waiting only for the energy and means to grapple with it. In everything that stands for the upbuilding of this laboratory, let us have cooperation with soul and zeal to make it effective and triumphant" (Whitman, address, 11 August 1903). Clearly, Whitman did not fully agree with Wilson that the success of the Naples Station lay "simply" with money.

Permanence, national support, cooperation, and independence have been achieved at the MBL to a remarkable extent. Yet as Whitman stressed, both money and a great deal of dedicated work by a large number of people remain necessary to maintain such enduring marine laboratories as the MBL and the Naples Station.

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THE WOODS HOLE LABORATORY SITE: HISTORY AND FUTURE ECOLOGY

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Abstract

The Woods Hole site of the Marine Biological Laboratory is adjacent to that chosen for work of the U. S. Fish Commission by Spencer F. Baird in 1871. In most ecological respects, it remains an excellent locus for marine research, with strong tidal currents ensuring a supply of pure sea water and with a reasonably diverse fauna and flora. Despite local environmental risks, there are grounds for cautious optimism that both Woods Hole and Naples (Ischia laboratory) can continue to provide opportunities for all kinds of biological research utilizing healthy marine organisms.

Introduction and History

The site of the Marine Biological Laboratory at Woods Hole is, in most ecological respects, a good one well-buffered by flowing sea water. In particular, it is excellently placed in relation both to the major oceanic circulation (Lillie, 1944) and to local tidal currents. It was chosen by Spencer F. Baird (possibly as early as 1863) as a site for work of the U. S. Fish Commission, and he began studies there in 1871 and 1875 (Conklin, 1944). The fisheries laboratory was built in 1885, and the adjacent MBL in 1888. On a narrow promontory between Buzzards Bay and Vineyard Sound, placed at an angle of the larger peninsula of Cape Cod, there are no large rivers near by, and Baird noted the purity of the local sea water, free from sediment or sewage contamination (Conklin, 1944).

Faunal Aspects

The waters off Cape Cod are affected by the Labrador Current to the north and the Gulf Stream to the south, and there are corresponding differences in at least 25% of the benthic fauna and rather more of the macrophytic algae. Thus we have both a cold-water *Strongylocentrotus* and a warm-water *Arbacia* available, providing ripe eggs in spring and in summer, respectively. In one respect, the intertidal and sublittoral faunas are somewhat impoverished. Since Cape Cod is entirely made up of glacial moraine there are no extensive rock outcrops, and so we lack *Octopus*, rock-boring bivalves, and certain species of hydroids, serpulids, barnacles, and opisthobranchs (including most species both of the beautiful nudibranchs and of the larger aplysiomorphs used in neural systems investigations). Parenthetically, it is clear that the different cephalopods available at the Stazione Zoologica (*Octopus*) and at the MBL (*Loligo*) led to markedly different emphases in neurobiological research over the last 45 years. The neural basis for capacity to learn or be trained, including controls utilizing split-brain techniques, were investigated at Naples, while the biophysics of neural membranes and chemical properties of the giant axon were investigated at Woods Hole.

Periodically, around Cape Cod, local grounds for squid, sea urchins, and certain fish and bivalves have been over-collected, but no faunal extinction can be attributed to MBL collectors. *Chaetopterus* may be the one locally collector-endangered genus at present (Valois, 1984). Recently, there has been some competition from commercial fishermen for squid, *Spisula,* and a few other forms. Lack of detailed knowledge of natural population dynamics (even demography) for these species makes it difficult to predict the effects of such sustained commercial cropping. Over the last century, the most extensive ecological changes in the area were the disease-caused decline of eelgrass (*Zostera*) beds between 1930 and 1960, and their recovery during the last 20 years. It seems probable that both a fungus, *Ophiobolus halimus,* and a slime-mold, *Labyrinthula macrocystis,* were important in this epidemic on both sides of the North Atlantic, although higher water temperatures may also have been involved. An excellent summary of the literature along with substantive data from Danish waters is provided by Rasmussen (1973). At Woods Hole as elsewhere, associated communities of invertebrates, including *Cumingia* (Russell-Hunter and Tashiro, 1985), became very rare for three decades and then required a further 20 years to approach their pre-1930 levels of abundance. No human pollution or other environmental modification has ever caused such widespread and long-lasting ecological changes.

Water Quality

Tidal currents run through the Woods Hole passage (between the Cape mainland and the Elizabeth Islands) reaching average maximum velocities four times daily, westwards of 3.6 knots and eastwards of 4.5 knots (White, 1984), and running at <0.8 knots for only 2.8 hours in each day [1 knot = 1.853 km/h]. Practicable extensions of the present sea water intake system of MBL into this tidal flow could protect pure sea water supply for the foreseeable future. A similar continuous supply of unpolluted sea water is ensured at the ecological laboratory (Bacci, 1969) of the Stazione Zoologica at Punta San Pietro on Ischia. Despite increasing residential building on Cape Cod, sewage contamination of MBL sea water is not a problem and the 1984–1986 sewer development for the Falmouth area further reduces the risk. In the near future, a more likely difficulty at Woods Hole could be ensuring an adequate supply of unpolluted fresh water (as has long been the case on Ischia).

Historically, both Woods Hole and Naples have been good sites for research on healthy marine organisms. The majority of the invertebrate species surveyed in 1871 by Spencer Baird's associate A. E. Verrill in the Vineyard Sound area are still there today. Similarly, Tomas (1984) could state that the flora and fauna of the sublittoral around Ischia were relatively unchanged from the time of Anton Dohrn. These historical continuities in natural populations provide grounds for cautious optimism regarding the future ecology of both areas. Despite this, we must increase our knowledge of natural life-cycles, demography, and ecology in the species we collect, and be prepared (for example, in the proposed Marine Resources Center at MBL) to move toward mariculture where appropriate. For the Cape Cod area, the only long-term environmental risk lies in the exploration for, and possible development of, offshore oil deposits on Georges Bank, but Woods Hole is somewhat protected by position and prevailing winds. Oil spills from vessels, even small ones, could affect many fragile habitats such as high salt marshes, but supertankers do not use Vineyard Sound or Buzzards Bay. Both cautious optimism for the future, and a sense of gratitude to Spencer F. Baird, Alpheus Hyatt, C. O. Whitman, and the others for picking the site, seem appropriate at this time.

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Along with my main charge to survey the history of invertebrate teaching at Woods Hole, Paul R. Gross and Seymour S. Cohen suggested that I prepare for discussion at the Ischia symposium this brief statement on the ecological setting and future of the MBL. I am grateful both to them and to Carmelo R. Tomas, my fellow-discussant from the Stazione Zoologica. Other acknowledgments are set out in my main paper (p. 88 of this issue).

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FROM WOODS HOLE TO THE WORLD: *THE BIOLOGICAL BULLETIN*

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Abstract

The Marine Biological Laboratory, Woods Hole, publishes *The Biological Bulletin:* a general research journal with an international circulation. It has been published continuously since 1902 (although its predecessors date from 1897), and there have been only eight editors. Characterized by its regularity of publication, diversity of contents, and editorial independence, it has not been a "house journal" for at least 55 years. Changes in its editorial policies have historically been minor. The MBL library has continued to benefit from approximately 650 serials received as "free" exchanges for the journal. For future historical research, an extensive archive of editorial correspondence will be provided.

Introduction

The journal, *The Biological Bulletin,* is a little younger than the laboratory at Woods Hole, but both are owned by the corporate membership of the Marine Biological Laboratory. To many members, unable to work at the laboratory, the conservatively printed grey cover contains the only tangible return for their continuing membership dues. Since 1902, with only minor changes of format but with a great diversity of contents, two volumes or six issues per year have appeared regularly. This *continuity* as a nonspecialist research journal has sustained library subscriptions both domestic and foreign, and also journal exchanges with learned societies and institutions throughout the world. Two examples of our cosmopolitan circulation are revealed by our inclusion in the citation and abstracting services run by the Polish Academy of Sciences in Warsaw, and the Indian Agricultural Research Council in New Delhi, both based on a precirculated contents proof for each issue. The age of the journal and its regularity of publication contribute to its worldwide circulation.

History

The general history of the MBL by Lillie (1944) is surprisingly unspecific about the journal, but Redfield (1941) provides an excellent review of its early days. Two volumes per year have been published continuously for 82 years (since the resumption of publication with volume 3 in Fall, 1902); although its predecessors date from 1897. Edited by the Director (C. O. Whitman) and members of the staff, two volumes of the *Zoological Bulletin* were published in 1897 and 1898, and the first two volumes of its successor *The Biological Bulletin* in 1900 and early 1901. Frank R. Lillie became Managing Editor with volume 3 in Fall 1902, and his editorial staff was listed as Conklin, Loeb, Morgan, Wheeler, Whitman, and Wilson. Lillie remained editor until 1927, and was succeeded in turn by: Carl R. Moore (1927–1930), Alfred C. Redfield (1930–1942), H. Burr Steinbach (1942–1950),

Donald P. Costello (1951–1968), W. D. Russell-Hunter (1968–1980), and Charles B. Metz (1980–). There have been no supplementary publications, and the history of publication of a single general journal from the MBL obviously differs from that of journal publishing at the Stazione Zoologica.

At Naples, three different serials were begun in 1879–80: an abstracting annual, a house journal, and a series of systematic monographs. Publication of the *Zoologischer Jahresbericht* helped the library of the Stazione, which received all the literature sent in for review. The journal publishing in-house work was the *Mittheilungen aus der Zoologischen Station zu Neapel* continued after 1916 as *Pubblicazioni della Stazione Zoologica di Napoli,* which has been split into two since 1979; *Marine Ecology (Pubbl. Staz. Zool. Napoli I)* and *History and Philosophy of the Life Sciences (Pubbl. Staz. Zool. Napoli II).* The magnificent monographic series, *Fauna und Flora des Golfes von Neapel,* has no Woods Hole equivalent.

Scope and Policy

The Biological Bulletin has always been a general rather than a specialist journal, publishing original research reports of intermediate length. It was first intended to be a companion journal to the *Journal of Morphology* providing for relatively rapid publication of shorter papers with simpler illustrations. From 1912 to 1929, it steadily became less of a "house journal." Since 1930, its editorial policies and reviewing procedures have been deliberately kept separate from both the administration and the elected trustees of MBL. Up to 1980, the managing editor was unpaid, and there was usually a single full-time editorial assistant (and some part-time help managing subscriptions). Home institutions of editors tolerated the demands (both in space and time) generated by their work as midwives for the scholarship of others.

To librarians and exchanging institutions, it remained associated with that select group of general journals of certain national academies and royal societies, characterized by Vannevar Bush as of greatest significance in the "invisible university" of world science. Frequently, new authors were surprised by contacts generated through its readership in Eastern Europe and in Asia. The MBL library has always benefitted from the 650 or so serials generated as "free" exchanges, and continuity both of these and of regular subscriptions has been influenced by regularity of publication and diversity of contents. Maintaining this diversity was the declared strategy of five of the editors and, in retrospect, changes in editorial policy were relatively trivial. A few good systematic papers were published in the periods 1930–1942 and 1968–1980, while taxonomy and systematics were deliberately excluded in 1912–1930 and in 1951–1968. Similarly, review papers were excluded from 1925–1980 although some were published before 1925 and after 1980. Abstracts of each summer's general meetings at MBL have been published for over 50 years, but the regular papers have more widespread origins. In the period 1950–1980, 19% of the papers published reported work done wholly or partly at MBL, 58% reported research conducted elsewhere in the U. S., and 23% had other international origins.

Archives

For future historians, an extensive archive will be provided by the files of completed editorial correspondence (including those for rejected papers) which have been preserved nearly completely from 1945, and partially from 1930. We have proposed that these files remain in their normal restricted use for reference in the

editorial office for 6 years, and then be "closed" for a further 20 years, before becoming available for approved historical research.

Acknowledgment

Along with my main charge to survey the history of invertebrate teaching at Woods Hole, Seymour S. Cohen suggested I prepare a brief historical statement on *The Biological Bulletin* for discussion at the Ischia symposium. I am grateful to him. Other acknowledgments are set out in my main paper (p. 88 of this issue).

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WHAT LABORATORIES FOR WHAT SCIENCE?

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Having examined the roles that the Zoological Station and the Marine Biological Laboratory have played in shaping ideas in biology since the turn of the century, it now seems appropriate to address the question of the future of marine biological laboratories, and, in fact, of biological research institutes in general. However, we should first determine the kind of science we want for the future. I believe that science should fit within a broad, non-restrictive, non-deterministic cultural framework. Indeed, science should become the focal point of a process of cultural renewal; a point of reference for future generations; and a driving force in all fields, scientific and non.

From many views, scientists of the 16th, 17th, and 18th centuries had more freedom than present-day scientists. Today researchers are no longer restricted by Church dogma, however governments, financial trusts, and military and economic demands impose more sophisticated and subtle pressures, which are totally unrelated to the needs of humanity.

This is not a plea to turn back the clock, but we must study the past to understand where we came from and how important achievements evolved to discover the roots that may nourish our future. The past can also help us to avoid repeating mistakes and to outline a future in which we are aware of the difficulties and responsibilities it entails.

There is obviously no easy remedy for all the problems that will arise. However, any new solutions or ideas will probably come from institutions that promote the growth of knowledge, that is, our schools and universities.

In the past, universities provided a broad, philosophical, humanistic, and scientific education, and were not as specialized as today. Specialization on the whole is acceptable, but it should not confine a person to a narrow corridor. New generations should be educated to be creative in solving the problems that will confront them. New researchers should be trained to have a dialectical attitude. After all, nature itself is dialectical.

Schools and universities must return to being forums where ideas are questioned and discussed, and they must produce people capable of using the most important tools available to mankind: culture and knowledge. I believe in a science that does not bind its fate to technology, but to the growth of knowledge.

After having presented an idea of what I believe is the cultural framework within which research should operate, I shall now turn to the organization of scientific institutes.

First of all, laboratories should not become isolated and closed structures; this would be detrimental to the quality of research and to researchers. This means encouraging international exchange between research laboratories and other cultural institutions.

I envisage research institutes as helping to define the cultural and material requirements necessary to improve the quality of life. Laboratories should not be limited to research but should stimulate the discussion of scientific and cultural topics in general. It is no exaggeration to say that many researchers have excellent

technical know-how, but lack a solid cultural background. Hence, the importance of non-specialized cultural activities such as symposia, workshops, and courses. By expanding the researcher's frontiers of knowledge, the quality of his research will improve.

Another aspect to be considered is the organization of research laboratories. To be efficient, an organization requires adequate funds and personnel, and well-defined programs. Furthermore, research groups consisting of scientists with different working experience should be encouraged so that scientific problems can be approached as impartially as possible. Scientists must also be morally, ethically, and financially stimulated.

We should also favor the development of science world-wide to counterbalance the tendency to reduce personnel. This brings me to funding for science. At present, financial backing is insufficient; scientists should demand that government funds now invested in armaments aimed at destroying life be employed for research aimed at improving the quality of life.

Lastly, research institutes should be known for their eagerness to learn, their creativity, and their ability to exploit all available intellectual energy. All this in turn should be directed towards meeting the various needs of humanity.

My comments so far concern not only the better functioning of research laboratories, but also offer guidelines aimed at improving the quality of life. It is my hope that science will contribute to arresting the advance of what I consider the barbaric tendency of focusing on material wealth and consumer items, rather than on the cultural and moral problems of modern man.

As in the past, science can determine many aspects of the future of humanity. Men of science must look beyond the limits of their own research activities and, by their culture and enlightenment, become intellectual leaders.

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